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Abstract

Teleosauroidea was a clade of successful, morphologically diverse ancient crocodylomorphs that were integral in coastal marine/lagoonal environments during the Jurassic. Within Teleosauroidea, the macrophagous/durophagous tribe Machimosaurini evolved specialized feeding strategies (e.g. hypertrophied jaw musculature; blunt, heavily ornamented dentition) and large body sizes (> 7 m), becoming an important component of Middle/Late Jurassic ecosystems. These ocean-dwelling giants are well known from the Callovian (*Lemmysuchus*) of Europe and the UK, and Kimmeridgian-Tithonian (*Machimosaurus*) of Europe and northern Africa. There are reports of fragmentary machimosaurin material from the Bathonian of Africa; however, the overall Bathonian teleosauroid material is poorly understood. While multiple specimens were described during the 19th and 20th centuries, little research has been done since. Here we re-describe two historically important Bathonian species from near Oxford, UK. We demonstrate that both '*Steneosaurus*' *larteti* and '*Steneosaurus*' *boutilieri* are indeed valid taxa and establish neotypes for both species and two new genera, *Deslongchampsina* and *Yvridiosuchus*. Our cladistic analysis finds *Yvridiosuchus boutilieri* as a basal member of Machimosaurini, and *Deslongchampsina larteti* to be closely related to *Steneosaurus heberti*. Interestingly, four distinct teleosauroid ecomorphotypes are present in the Bathonian of Europe, and teleosauroid ecomorphological diversity continued throughout the Callovian and Kimmeridgian/Tithonian in Europe and England.

Keywords: Bathonian – Crocodylomorpha – Teleosauroidea – Thalattosuchia

Introduction

Teleosauroids (Thalattosuchia) were a unique group of distant extinct relatives of modern crocodiles that inhabited marine and brackish ecosystems throughout the Jurassic (Buffetaut, et al., 1981; Buffetaut, 1982; Andrews, 1913; Hua, 1999; Foffa et al., 2015, in press; Johnson et al., 2015, 2017, 2018; Martin et al., 2016) and Early Cretaceous (Fanti et al., 2016). This near-global group of ancient crocodylomorphs have often been regarded as the Jurassic marine equivalents of extant gavials, due to many species having an elongate and tubular snout, high tooth count and dorsally directed orbits, which is suggestive of a primarily piscivorous diet (Andrews, 1909, 1913; Buffetaut, 1982).

However, within Teleosauroidea, the tribe Machimosaurini is characterised by blunt tooth crowns with serrated carinae and extensive enamel ornamentation; proportionally shorter snouts and lower tooth count; and proportionally anteroposteriorly and mediolaterally enlarged supratemporal fenestrae, all of which suggest a macrophagous-durophagous lifestyle (Eudes-Deslongchamps, 1864, 1867, 1869; Andrews, 1909, 1913; Buffetaut, 1982; Massare, 1987; Hua et al., 1994; Hua & Buffetaut, 1997; Vignaud, 1997; Martin & Vincent, 2013; Young et al., 2014a, 2014b, 2015a, 2015b; Fanti et al., 2016; Jouve et al., 2016; Johnson et al., 2017; Foffa et al., 2018a). During the Middle Jurassic, machimosaurins were relatively rare compared to other teleosauroids, with isolated tooth crowns and indeterminate material known from the Bathonian of England, France and Morocco (Young et al., 2014a; Jouve et al., 2016), and *Lemmysuchus obtusidens* (Johnson et al., 2017) from the Callovian of England and France (Andrews, 1909, 1913; Young et al., 2016; Johnson et al., 2017). The Oxfordian is a poorly sampled stage for teleosauroids, but *L*. cf. *obtusidens* and *Machimosaurus* sp. are known from England and France respectively (Young et al., 2014a; Foffa et al., 2015, 2018b). However, by the Kimmeridgian and Tithonian multiple species of *Machimosaurus*

are found across Europe (Sauvage & Liénard, 1879; Vignaud et al., 1993; Vignaud, 1995; Hua, 1996, 1999; Martin & Vincent, 2013; Young et al., 2014a, 2014b). By the end Kimmeridgian-earliest Tithonian, they had evolved into species adapted to living in high-energy environments (*Machimosaurus mosae* Sauvage & Liénard, 1879: Hua, 1999; Young et al., 2014a) and others suited to life in open seas (*Machimosaurus hugii* von Meyer, 1837: Krebs, 1967; Young et al., 2014a).

Unfortunately, the machimosaurin material found from the Bathonian of Europe is poorly understood in terms of morphology, taxonomy and phylogenetics. While a handful of specimens from the Cornbrash Formation of England and Arromanches, France were found and studied during the 19th and mid-20th centuries (see de la Bêche & Conybeare, 1821; Eudes-Deslongchamps, 1866, 1868; Eudes-Deslongchamps, 1867-69; Phillips, 1871; Phizackerely, 1951), few studies since have addressed them (e.g. Young et al., 2014a), due to few complete specimens and confusing taxonomic and phylogenetic issues.

Herein we review two historically important teleosauroid taxa comprising of near complete skulls housed in the Oxford University Museum of Natural History (OUMNH) from nearshore marine deposits of the Bathonian of England, provide detailed re-descriptions and establish two new genera. Using the latest phylogenetic analyses, we are able to test the relationships of these two new taxa within Teleosauroidea, and show that durophagous/macrophagous taxa were present within the Bathonian of the UK.

Historical Background: '*Steneosaurus*' *larteti*

The taxonomic history of '*Steneosaurus*' *larteti* is convoluted. The holotype material comprised of a semi-complete skull, which was first named and described as *Teleosaurus*

larteti by Jacques Amand Eudes-Deslongchamps (1866). The holotype was named after Mr. Lartet, "*notre grand paléontologiste français*" ["…our great French palaeontologist…"] (Eudes-Deslongchamps, 1867-69). The specimen (which also included a portion of the lower jaw, pelvis, hindlimb, two vertebrae and some dorsal osteoderms) was initially acquired by politician Mr. Abel Vautier (when and how is unclear); he then gave it to J. A. Eudes-Deslongchamps, who had it prepared, presumably by Mr. Stahl, the chief preparator ["*chef du moulage*"] (of which institution or university is not mentioned) (Eudes-Deslongchamps, 1867-69). The specimen was then reportedly stored in the collection of the Sorbonne Museum in Toulouse, France. J. A. Eudes-Deslongchamps (1868) later changed the generic name to *Steneosaurus*; why he did so is unclear. His son Eugène Eudes-Deslongchamps (1867-69) re-described and re-figured the specimen in his famous '*Notes Paléontologiques*'. E. Eudes-Deslongchamps (1868, 1867-69) also briefly referred to specimens from both England and Germany (one of these is thought to be OUMNH J.29851) as '*S.*' *larteti*.

Phillips (1871) briefly referred to a handful of teleosauroid material (presumably including the English '*S.*' *larteti*) housed in the Oxford Museum (now known as the OUMNH) as *Teleosaurus brevidens* n. sp., although he did not explicitly mention which specimen(s) he was referring to, and made no mention of comparisons to the two Eudes-Deslongchamps' French specimens. Lydekker (1888) mentioned additional specimens, from both France and the UK, as pertaining to '*S.*' *larteti*, and Auer (1890) referred to a Callovian specimen (housed at the Eberhard Karls Universität Tübingen) as '*Steneosaurus*' *Larteti* var. *Kokeni*. Vignaud (1995) stated that the French holotype described by J.A Eudes-Deslongchamps (1866) was eventually presumed destroyed during the bombing of Caen in 1944. During the mid-1900s, Phizackerely (1951) established a new species, *Steneosaurus meretrix* nov. sp. (the naming controversy of *S. meretrix* will be discussed in the next section), referred OUMNH J.29851 (as well as several other Oxford specimens) to that

species, and designated it as the paratype. Buffetaut and Thierry (1977) referred to a specimen, discovered by M. Détouillon, from Talant, France, as '*Steneosaurus*' *larteti*, which comprised of a nearly skull and mandible, six vertebrae and an assortment of osteoderms. However, there is no reference as to where this specimen was or is currently housed. Young et al. (2014a) also figured and briefly referred to both OUMNH J.29850 and OUMNH J.29851 as '*S.*' *larteti*.

Historical Background: '*Steneosaurus*' *boutilieri*

1.1 Early to mid-1800s, Notes Paléontologiques, and the mystery of Crocodilus oxoniensis

As with '*Steneosaurus*' *larteti*, the history of '*Steneosaurus*' *boutilieri* is complicated, but with perhaps a more confusing origin. De la Bêche and Conybeare (1821) mentioned the discovery of a partial crocodile skull from the Cornbrash Formation of Gibraltar, near Oxford. This skull was very briefly mentioned again by Conybeare and Phillips (1822) and then largely neglected. It was not until E. Eudes -Deslongchamps' '*Notes Paléontologiques*' (1867-69) that this specimen was mentioned again. E. Eudes-Deslongchamps (1867-69, p. 230) stated "*…j'ai pu étudier, dans la collection d'anatomie comparée du Muséum, un modèle en plâtre d'une tête presque complète avec sa mâchoire infé rieure, qui a été recueillie dans le cornbrash des environs d'Oxford (Angleterre). A cette pièce, portant sous le numéro de catalogue vm-2357 l'indication suivante, Crocodilus oxoniensis (Conybeare) , était annexée une petite note pro bablement de la main de M. de Blainville et portant ces mots : « Trouvé près d'Oxford dans le calcaire oolithique dit cornbrash, donné par l'institution de Bristol, probablement une des espèces d'Honfleur*" ["… I have been able to study, in the Museum's Comparative Anatomy Collection, a plaster model of an almost

complete head with its lower jaw, which has been collected in the Cornbrash of the neighbourhood [of] Oxford (England). To this piece, bearing under the catalogue number vm-2357, the following indication, *Crocodilus oxoniensis* (Conybeare), was attached, a small note probably by the hand of M. de Blainville and bearing these words: "Found near Oxford in oolitic limestone known as Cornbrash, given by the institution of Bristol, probably one of Honfleur's species"]. In his monograph, E. Eudes-Deslongchamps (1867-69) disagreed with the naming of *C. oxoniensis*, claiming that he could not find any information pertaining to the description of this species, and that it was therefore invalid. Eudes-Deslongchamps (1867-69 p. 231) also stated the following about the *C. oxoniensis* 'holotype' (OUMNH J.1401): "*c'est donc probablement un simple nom de catalogue donné dans une collection publique, et je pense que dans le cas où l'on viendrait à reconnaître que l'espèce des environs d'Oxford est la même que celle de Longues, on devrait les désigner l'une et l'autre sous le nom de* Steneosaurus Boutilieri " ["… [so] it's probably a simple catalogue name given in a public collection, and I think that, in the event that we come to recognize that the species around Oxford is the same as that of Longues [the area where the French '*S.*' *boutilieri* holotype was found], we should designate each under the name of *Steneosaurus Boutilieri*"].

Since de la Bêche and Conybeare (1821) never explicitly used the species *oxoniensis* in their work, it could be argued that it is indeed not a valid species name, but rather one only present on specimen labels. According to Article 12.2.7 of the Code of the International Commission on Zoological Nomenclature (ICZN), when publishing names before 1931, "*the proposal of a new genus-group name or of a new species-group name in association with an illustration of the taxon being named, or with a bibliographic reference to such an illustration, even if the illustration is contained in a work published before 1758, or in one that is not consistently binominal, or in one that has been suppressed by the Commission (unless the Commission has ruled that the work is to be treated as not having been published*

[Art. 8.7])" is perceived as valid. De la Bêche and Conybeare (1821) did not designate a new species, nor did they provide an indicative illustration or drawing of the crocodile skull from near Oxford; the name itself was only given on a specimen label. Therefore, the name *C. oxoniensis* is not valid under the ICZN Code. Vignaud (1995: 186) mentioned that Eudes-Deslongchamps considered OUMNH J.1401 as "*appartenant à la même espèce*" ["belonging to the same species"] as the French holotype. A Mr. Boutillier, a former merchant who resided at Roncherolles, gave the holotype of '*S.*' *boutilieri* to the younger Eudes-Deslongchamps (when is unknown), as he had acquired this fossil from Mr. Sœmann, a man "*très intelligent, vient souvent dans nos pays récolter des fossiles pour le compte de son patron*" [*"…very intelligent, often coming [to] our country to collect fossils on behalf of his boss…*"] (Eudes-Deslongchamps 1866: 121). When initially describing '*S.*' *boutilieri*, J. A. Eudes-Deslongchamps (1868) incorporated material from both the French 'holotype' and OUMNH J.1401; E. Eudes-Deslongchamps (1867-69) also re-described '*S.*' *boutilieri* using these specimens. In addition, Woodward (1885) explicitly reports that the cast (OUMNH J.1401) in Oxford has the names of *Crocodilus oxoniensis* Conybeare and *Steneosaurus oxoniensis* de la Beche. Woodward (1885: 501) also writes that "*Mr. Edward Wilson, to whose kindness the writer is indebted for particulars of the Crocodilian fossils now in the Bristol Museum, is unable to discover any such label in the collection; and the present whereabouts of the original specimen seems to be unknown*". Based on Woodward's (1885) comments, it appears as though the epithet 'oxoniensis' was never formally published, and thus is an invalid name (a nomen nudum).

1.2 The late 1800s

As mentioned previously, Phillips (1871) named and described a new species, *Teleosaurus brevidens*, using teleosauroid material housed in the Oxford Museum (however,

he was unclear which exact specimen(s) he referred to). He mentioned these specimens as being "*observed in Stonesfield and some other places in the Great oolite near Oxford, [as] Enslow Bridge and Kidlington*" (Phillips 1871: 184). On pages 184 to 185, figured in Diagram No. XLII/fig. 1 (Phillips 1871), he described the teeth of *T. brevidens* as "*rather short [teeth]…a little curved, uniformly striated, the striae growing more prominent toward the point and finer toward the base… [a] slight trace of bicarination on these teeth, near the apex, which is usually blunt…*" and regarded these features as among the defining characteristics of *T. brevidens* (Phillips appears to be referring to the anastomosing pattern that is characteristic of machimosaurin teeth). Presumably, Phillips (1871) was referring to OUMNH J.29850 and/or OUMNH J.1403, as he referred to not only the teeth but the skull and palatal material as well.

Hulke (1877) described and figured a new species in dorsal view, *Steneosaurus stephani* nov. sp. (NHMUK PV OR 49126), also present in the Cornbrash Formationm and found in Closworth, Dorsetshire by Mr. Darell Stephens. Hulke (1877) compared it to the descriptions of '*S.*' *larteti*, '*S.*' *boutilieri* and *Steneosaurus megistorhynchus* Geoffroy, 1831 (emend. Eudes-Deslongchamps, 1866), given by E. Eudes-Deslongchamps (1867-69). Interestingly, Hulke (1877: 29) also briefly refers to *Steneosaurus* (*Crocodilus*) *oxoniensis* in his comparisons, and writes as if E. Eudes-Deslongchamps used the name as well (["…*which M. Deslongchamps regards as the mature form of* Steneosaurus Oxoniensis…"]). However, as mentioned previously, E. Eudes-Deslongchamps (1867-69) did not find *oxoniensis* as valid and referred to it as *boutilieri*. However, we agree with Hulke (1877) and consider *S. stephani* to be a separate and distinct species (see Discussion).

1.3 The 1900s to present day

In the early 20th century, Watson (1911) briefly described the palatal view of *S. stephani* (NHMUK PV OR 49126), which was initially neglected by Hulke (1877). Watson (1911, No. 18: 3) stated: "*Eudes-Deslongchamps figures a plaster cast of a skull [OUMNH J.1401] from the English Cornbrash which he identifies with his S. Boutilieri. This skull consists almost entirely of rostrum and is hence rather difficult to compare with S. stephani: so far as corresponding portions of the two skulls occur, they agree, and it is probable that they belong to the same species. The Bristol Museum contains another copy of this cast, and I found there a cast of the back of a Steneosaur skull which may belong to it; it agrees closely with S. stephani, but as there is no real evidence that it belongs to the snout, I think it is preferable to keep the name stephani for the Closworth skull.*"

It was not until Phizackerley's (1951) short monograph on teleosauroid specimens from Oxford that '*S.*' *boutilieri*, *T. brevidens* or the de la Bêche & Conybeare specimen was one again examined in any detail. Phizackerely (1951: 1184) initially referred to OUMNH J.29850 as being the type specimen of *T. brevidens* (note that, in 1951, the specimen was housed in the Department of Zoology at Oxford, so the specimen number was 1639/1; when it was moved to the Earth Sciences collection in the museum and given its current specimen number is unknown). Curiously, Phizackerley (1951: 1185) then stated that type material of *T. brevidens* was inaccessible, but then used1639/1 (OUMNH J.29850) as the type specimen of his new species '*Steneosaurus*' *meretrix*. This very odd situation means that the type specimen of '*S.*' *meretrix* was already the type specimen of *T. brevidens*, thus making them objective synonyms. Thus, both *T. brevidens* and '*S.*' *meretrix* are considered as invalid species, and are junior synonyms of 'S.' boutilieri.

Steel (1973) and Vignaud (1995, 1997) referred to OUMNH J.1401 (the '*oxoniensis*' skull) and the *T. brevidens*/ '*S.*' *meretrix* holotype (OUMNH J.29850) as '*S.*' *boutilieri*,

although Vignaud (1997) referred to OUMNH J.1401 as *C. oxoniensis*. Godefroit (1996) also briefly mentions E. Eudes-Deslongchamps' (1867-69) holotype of '*S.*' *boutilieri* (as well as Phizackerley's (1951) work on the aforementioned Oxford specimens and Hulke's (1877) *S. stephani*) in comparison with a new specimen of S. megistorhynchus. Vignaud (1998) also highlighted the characteristic robust shape of the teeth seen in '*S.*' *boutilieri*.

Geology

The Great Oolite Group (GOG) is a Middle Jurassic (Bathonian) lithostratigraphic unit that is well known from extensive exposures in central England, UK. The GOG consists of three formations that are, from youngest to oldest, the Cornbrash Formation, the Forest Marble Formation, and the White Limestone Formation (Palmer & Jenkyns, 1975; Sellwood et al., 1985). Both the Forest Marble Formation and the White Limestone Formation were primarily deposited by laterally migrating tidal channels in an intertidal environment (Klein, 1963, 1965; Palmer & Jenkyns, 1975). Several important fossils are known from the Great Oolite Group, including pterosaurs (O'Sullivan and Martill, 2018), crocodylomorphs (de la Bêche and Conybeare, 1821; Eudes-Deslongchamps, 1867-69), dinosaur remains (Woodward 1910; Benson 2010) and reptilian eggs (Buckman, 1860).

The Cornbrash Formation (CF) is a Bathonian–Callovian (Middle Jurassic) lithostratigraphic unit that underlies the Oxford Clay Formation (OCF) (Wright, 1977). This stratigraphic section consists of medium- to fine-grained limestone that is bioturbated, yields some reptilian (Hulke, 1877; Benton and Spencer, 1995) and many trace (e.g. Powell and Riding, 2016) fossils and stretches from the Weymouth area to the Scarborough area in the UK (Cox & Sumbler, 2002), similar to the OCF. The CF is comprised of two main units (the

Cornbrash Limestone and the Cornbrash Shales) which form a transgressional marine cycle and marks the first marine invasion of the Jurassic delta subsequent to that represented by the Middle Bajocian Scarborough Beds (Wright, 1977). The CF in England is also correlative with 'Fuller's Earth inférieur' in France (see Vignaud, 1995). All currently known English specimens of '*S.*' *boutilieri* (e.g. OUMNH J.1401, OUMNH J.29850) and '*S.*' *larteti* (OUMNH J.29851) were found in the CF.

The area of Arromanches is located near the northern coast of France, and has several localities in which Jurassic rocks are exposed (de la Bêche, 1822). One particular rock unit is the Caen Limestone, which dates back to the Early to Mid-Bathonian (Rioult, 1961; Fily, 1978) and represents a shallow lagoonal environment. The Caen Limestone includes the *Zigzagiceras zigzag*, *Asphinctites tenuiplicatus* and *Procerites progracilis* ammonite Zones from the early to middle Bathonian (O'Dogherty et al., 2000; Sandoval et al., 2001; Moyne & Neige, 2007), and is represented by fossils of crocodylomorphs (Eudes-Deslongchamps, 1867-69) and multiple invertebrates (e.g. Lyell, 1840; Pavia et al, 2013). A second locality is Longues-sur-Mer (Calvados, Normandy), which includes sections of Bathonian oolitic sandstones and limestones (de la Bêche, 1822; Benabdellouahed et al., 2014). These oolitic sediments include the *Oxycerites* cf. *orbis* and *Clydoniceras discusa* ammonite Zones from the middle to late Bathonian (Sandoval et al., 2001; Roy et al., 2007; Scheck-Wenderoth et al., 2008). It is near Longues-sur-Mer that the holotype of '*S.*' *boutilieri* was presumably collected (Eudes-Deslongchamps, 1867-69), at the "*sommet de la Grande Oolithe*" in the *Oxycerites* cf. *orbis* or *Clydoniceras discus* ammonite Zones (Vignaud, 1995). The holotype of '*S.*' *larteti* came from the "*Calcaire de Caen ou "Fuller's earth inférieur*" in either the *Zigzagiceras zigzag*, *Asphinctites tenuiplicatus* and *Procerites progracilis* ammonite Zones (Eudes-Deslongchamps, 1867-69; Vignaud, 1995).

Abbreviations

Institutional: **CAMSM**, Sedgewick Museum, Cambridge, UK; **IRSNB**, Institut Royal des Sciences Naturelles de Bruxelles, Belgium; **GPIT**, Paläontologische Sammlung der Eberhard Karls Universität Tübingen, Germany; **IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; **LPP (PALEVOPRIM-CVCU)**, Institut de paléoprimatologie, paléontologie, humaine; évolution et paléoenvironnements Université de Poitiers, Poitiers, France; **MG**, Museu Geológico, Lisbon, Portugal; **MHNM**, Muséum d'Histoire Naturelle de Marrakech, Morocco; **MNHN**, Muséum national d'histoire naturelle, Paris, France; **MNHNL**, Musée national d'histoire naturelle, Luxembourg; **MMG**, Staaliches Museum für Mineralogie und Geologie, Dresden, Germany; **NHMUK**, Natural History Museum, London, UK; **NOTNH**, Nottingham Natural History Museum, Nottingham, UK; **ONM**, Musée de l'Office National Des Mines, Tunis, Tunisia; **OUMNH**, Oxford University Museum of Natural History, Oxford, UK;. **PETMG**, Peterborough Museum and Art Gallery, Peterborough, UK; **SMNS**, Staatliches Museum für Naturkunde Stuttgart, Baden-Württemberg, Germany.

Anatomical: **an**, angular; **anas**, anastomosing pattern; **antorb f**, antorbital fenestra; **art**, articular; **basiocc**, basioccipital; **?basisph**, possible basisphenoid; **basisph**, basisphenoid; **car**, carina; **cnXII**, cranial nerve XII; **cor**, coranoid; **cor gr**, coronoid groove; **D4**, fourth dentary alveolus; **D16**, sixteenth dentary alveolus; **den**, dentary; **dor o**, dorsal osteoderm; **ectopt**, ectopterygoid; **exocc**, exoccipital- opisthotic; **f**, frontal; **f m**, foramen magnum; **?j**, possible jugal; **j**, jugal; **l**, lacrimal; **Mec gr**, Meckelian groove; **M1**, first maxillary alveolus; **M12**, twelfth maxillary alveolus; **M16**, sixteenth maxillary alveolus; **M18**, eighteenth maxillary alveolus; **mx**, maxilla; **n**, nasal; **P3**, third premaxillary alveolus; **occ con**, occipital

condyle; **orb**, orbit; **p**, parietal; **pal**, palatine; **pmx**, premaxilla; **porb**, postorbital; **prf**, prefrontal; **pt**, pterygoid; **q**, quadrate; **qj**, quadratojugal; rec p, reception pit; **retro art**, retroarticular process; **spl**, splenial; **sq**, squamosal; **subor**, suborbital fenestra; **supraocc**, supraoccipital, **sur**, surangular.

Systematic Palaeontology

Crocodylomorpha Hay, 1930 (sensu Nesbitt, 2011)

Thalattosuchia Fraas, 1901 (sensu Young & Andrade, 2009)

Teleosauroidea Geoffroy Saint-Hilaire, 1831 (sensu Young and Andrade, 2009)

Deslongchampsina Gen. Nov.

Type species: *Teleosaurus larteti* Eudes-Deslongchamps, 1866 [following recommendation 67B of the ICZN Code]. Now referred to as *Deslongchampsina larteti* (Eudes-Deslongchamps, 1866) comb. nov.

Diagnosis: same as the only known species (monotypic genus).

Etymology: named in honour of father and son French naturalists Jacques Amand and Eugène Eudes-Deslongchamps, who thoroughly described the holotype specimen (in addition to numerous other teleosauroid taxa during the latter 1800s).

Deslongchampsina larteti (Fig. 1)

v 1866* *Teleosaurus larteti* nov. sp.; J.A. E-Deslongchamps, p.80-85, pl.5 fig.6

v 1868b *Steneosaurus larteti* (Deslongchamps) comb. nov., J.A. E-Deslongchamps, p.124

v 1867-69 *Steneosaurus larteti* (Deslongchamps); E. E-Deslongchamps, p.202, pl.14 fig 1-4

v 1870 *Steneosaurus larteti* (Deslongchamps); E. E-Deslongchamps, p.325, pl.4 fig.1-4

Vp. 1871 *Teleosaurus brevidens* n. sp.; Philips, p.186

v 1875 *Steneosaurus larteti* (Deslongchamps); Huxley, p. 436, pl. 19

(?) 1888 '*Steneosaurus*' de Parmilieu; Larrazet, p.8-15, pl.1-2

v 1888 *Steneosaurus larteti* (Deslongchamps); Lydekker, p.114

1909 *Steneosaurus Larteti* var. *Kokeni* (sic) n. var.; Auer, p.256, pl.22-23

1914 *Steneosaurus larteti* (sic) (Deslongchamps); Dreverman, p.42-43, fig.5

v 1936 *Steneosaurus larteti* (Deslongchamps); Kuhn, p.36

v 1951 *Steneosaurus meretrix* n. sp.; Phizackerley, p.1185-1187, fig.4-6

v 1962 *Steneosaurus larteti* (Deslongchamps); Krebs, p.15

v 1973 *Steneosaurus larteti* (Deslongchamps); Steel, p.31

v 1977 *Steneosaurus larteti* (Deslongchamps); Buffetaut & Thierry, p.158, fig.3

v 1982 *Steneosaurus larteti* (Deslongchamps); Buffetaut, p.20

v 1995 *Steneosaurus larteti* (Deslongchamps); Vignaud, p.187-188, pl.3

v 1996 *Steneosaurus larteti* (Deslongchamps); Godefroit et al., p.98

1998 *Steneosaurus larteti* (Deslongchamps); Mazin et al.,

v 1998 *Steneosaurus larteti* (Deslongchamps); Vignaud, p.22-23

v 2014 *Steneosaurus larteti* (Deslongchamps); Young et al., p.3

Holotype: A partial skull that was associated with a partial symphyseal section of the mandible, pelvis, hindlimb, two vertebrae (position in the axial skeleton unknown) and various dorsal osteoderms. Destroyed in 1944.

Holotype locality and horizon: "*Fuller's Earth inférieur*", Calvados, France. Bathonian, Middle Jurassic.

Neotype: OUMNH J.29851, comprising a partial skull, broken into two pieces.

Designation of neotype: Herein we formally designate OUMNH J.29851 as the neotype of *Deslongchampsina larteti*. In order to be in full accordance of Article 75 of the ICZN Code, in particular Article 75.3, we make the following statements:

1. This designation is made with the express purpose of clarifying the taxonomic status of *Deslongchampsina larteti*.

2. Our statement of the characters that we regard as differentiating *Deslongchampsina larteti* from other taxa is given by the species diagnosis below.

3. The neotype can be recognised through both the description below and Fig. 1.

4. The holotype is presumed destroyed in 1944 during the bombing of Caen.

5. The holotype had a partial skull; the description and figure given by J. A. Eudes-Deslongchamps (1866) show it was a gracile, mesorostrine skull with rounded (little constricted) premaxillae, oval orbits, large antorbital fenestrae, robust and pointed teeth and slight but noticeable ornamentation. As such, the neotype is consistent with what is known of the former name-bearing type.
6. Unfortunately, the neotype is not from the same locality or country as the holotype. However, both types are from the same age (Bathonian) and relative formation (the Cornbrash Formation in England is correlative with "*Fuller's Earth inférieur*" in France), and have both been referred to as the same species (see Historical Background).
7. The neotype is the property of a recognized scientific institution, OUMNH, which maintains a research collection with proper facilities for preserving name-bearing types, and is accessible for study.

Neotype locality and horizon: Cornbrash Formation, Great Oolite Group, Enslow Bridge, UK.
Etymology: Named after Mr. Lartet, who gave the fossil to J. A. Eudes-Deslongchamps to study.

Emended diagnosis: Teleosauroid crocodylomorph with the following unique combination of characters among teleosauroids [autapomorphic characters indicated by an asterisk (*)]: mesorostrine snout (rostrum under 68% of total skull length) (shared with '*Steneosaurus*' *brevior* Phillips, 1876, the Chinese teleosauroid IVPP V 10098, *Steneosaurus edwardsi* Eudes-Deslongchamps, 1868c, and Machimosaurini); faint constriction of the premaxillae posterior to the external nares, giving the premaxillae a rounded, 'globular' appearance*; mediolaterally thin posterior processes of the nasals*; gradual and well-developed anteroventral sloping of the nasals*; presence of large, elongated antorbital fenestrae, and

internal antorbital fenestra between 25-50% of the length of the orbit (shared with *Steneosaurus gracilirostris* Westphal, 1961, and '*S.*' *brevior*); frontal width subequal with orbital width (shared with the Chinese teleosauroid previously referred to as *Peipehsuchus* (see Li, 1994), *Mycterosuchus nasutus* Andrews, 1913, *Steneosaurus heberti* Morel de Glasville, 1876, *Yvridiosuchus boutilieri*, *Machimosaurus hugii* and *Machimosaurus rex* Fanti et al., 2016); small basioccipital tuberosities (similar to *Bathysuchus megarhinus* Hulke, 1871; [Foffa et al., in press]); palatine anterior margin terminates level to 21st maxillary alveoli, or more distal alveoli (shared with *Steneosaurus leedsi* Andrews, 1909, *Myc*. *nasutus* and *B*. *megarhinus*); four premaxillary alveoli; large, robust, non-compressed teeth with a pointed apex and high relief enamel ridges (similar to *Steneosaurus edwardsi*).

Description

A partial skull, broken into two pieces (rostrum and occipital), is the neotype of *Deslongchampsina larteti* (Fig. 1). The specimen is slightly dorsoventrally crushed in the anterior premaxillae and postorbital areas, but is overall relatively well preserved. The two pieces do not fit together exactly, as there is a small anterior part of the occipital piece not preserved. The skull is approximately 51 cm long from the anterior-most tip of the rostrum to the anterior margin of the orbits.

Premaxillae: The premaxillae (Fig. 1A-H) are relatively large and robust, surrounding the external narial opening. The external nares are oriented anterodorsally, laterally expanded and their posterior margins do not reach beyond the third premaxillary alveolar pair. Situated laterally to the external nares, there are a few shallow, circular foraminae. The anterior two-thirds of the premaxilla is anteroposteriorly shortened and the anterior margin is ventrally deflected (giving the snout a scoop-like appearance, although not as pronounced as in *Mycterosuchus* (NHMUK PV R 2617) or an unnumbered LPP *Bathysuchus* specimen). In

dorsal view, the premaxilla-maxilla suture is subcircular and slightly interdigitating (Fig. 1A-B). There is very little constriction of the premaxillae posterior to the external nares (Figs. 1, 3. 1A-B), which is not influenced by the slight dorsoventral crushing of the premaxillae. The Due to this lack of constriction, the premaxillae appear almost globular in dorsal and ventral views, which differs from other teleosauroids (e.g. *S. leedsi* NHMUK PV R 3806; *Steneosaurus bollensis* Jäger, 1828, SMNS 51563, MMG BwJ 565; Mac. buffetauti SMNS 91415) (Fig. 10). In ventral view, the incisive foramen (=naso-oral fenestra) is relatively large and subcircular, and is situated in the middle of the suture of the premaxillae. There are four alveoli present (Fig. 1C-D), similar to most teleosauroids (e.g. '*S.*' *brevior* NHMUK PV OR 14781; *S. leedsi* NHMUK PV R 3806; *S. edwardsi* NHMUK PV R 3701) but different from *Platysuchus multiscrobiculatus* Berckhemer, 1929, *Bathysuchus* (which both have five) and *Machimosaurus* species (which have three). The first two alveoli are nearly confluent with a thin interalveolar lamina separating them. Both premaxillae are ornamented with conspicuous grooves on the external surfaces (Fig. 1A-B, E-H).

Maxillae: The maxillae (Fig. 1A-H) form a substantial part of the rostrum: they are elongate, transversely narrow, anteriorly separated by the premaxillae, and their lateral margins are sub-parallel in dorsal view. The nasals are separated from the premaxillae by the maxillae. In dorsal and lateral views, the maxilla is ornamented with a few small pits and more numerous, larger grooves (Figs. 1A-B, E-H). In addition, there is a parallel line of medium-sized, semi-circular foramina dorsal to the maxillary ventral margin (Fig. 1E-H), similar to *S. edwardsi* (PETMG R178, NHMUK PV 2865) and *S. leedsi* (NHMUK PV R 3806) and differing from machimosaurins (which have two lines of foraminae). The precise maxillary tooth count is difficult to determine, but there are at least 27 alveolar pairs, with the maxillary alveoli being very large and circular to subcircular in shape. The first maxillary alveolus is slightly laterally oriented, best seen in left lateral view (Fig. 1E-F); the positioning of this alveolus does not

appear to have been influenced by dorsoventral crushing. The maxillary tooth row ends anterior to the anterior-most border of the sub-orbital fenestra. Reception pits for the dentary teeth are deep in the anterior portion of the maxilla but disappear when progressing posteriorly, similar to *S. edwardsi* (NHMUK PV R 2865, PETMG R178) and *S. heberti* (MNHN.F 1890-13). In ventral view (Fig. 1C-D), the maxilla is smooth and unornamented, and the palatal processes meet in the midline expanding anteriorly and posteriorly. The maxilla forms the anterolateral margin of the suborbital fenestra (seen only in the anterior right) (Fig. 1C-D). Faint palatal canals are also present laterally to the midline suture.

Jugals: The jugals (Fig. 1E-H) are triradiate and form the lateral border of the orbit, as in other teleosauroids (e.g. *S. leedsi* NHMUK PV R 3806; *S. bollensis* GPIT-RE-9425, SMNS 51957; the Chinese teleosauroid IVPP V 10098; *L. obtusidens* NHMUK PV R 3168). The left anterior jugal is covered by a specimen label (Fig. 1E). The postorbital-jugal contact (best seen in right lateral view) appears to be anteroposteriorly straight (Fig. 1G-H). It is difficult to discern the right maxillojugal contact due to a couple of large cracks in the area (Fig. 1G-H); however, the anterior jugal does not extend anteriorly past the orbits as in *L. obtusidens* (NHMUK PV R 3168, PETMG R39) or *S. edwardsi* (PETMG R178). The posterior parts of both jugals are not preserved, and the quadratojugal-jugal contact is not seen.

Nasals: The large, triangular nasals (Fig. 1A-B, E-H) are exposed on the dorsal surface of the posterior rostrum and orbital area. The anterior nasals are mediolaterally narrow and the lateral margins are strongly confluent. The nasal anterior processes are approximately one-third of the posterior area of the rostrum and have a well-developed near-parallel sutural contact with the maxillae. The nasals also have a strongly interdigitating contact with both the prefrontals and frontal. The posterior processes of the nasals are mediolaterally thin and are constricted by the prefrontals and frontal (Fig. 1A-B) relative to other teleosauroids (e.g.

S. leedsi NHMUK PV R 3806; *S. bollensis* SMNS 20283, SMNS 51563). There is a slight yet noticeable midline concavity ('midline trench') and a well-developed internarial suture (especially in the posterior region), suggesting that the nasals are unfused (differing from *L. obtusidens* NHMUK PV R 3168). In lateral view, the posterior nasals have a well-developed, gradual anteroventral 'slope' (Fig. 1E-H), differing from the abrupt 'dome' seen in *L. obtusidens* (e.g. NHMUK PV R 3168, NOTNH FS3361).

Prefrontals: The prefrontals (Fig. 1A-B, E-H) are sub-triangular in shape and longer than wide in dorsal view. The prefrontal forms the anteromedial border of the orbits, and contacts the nasal and frontal medially and the lacrimal laterally (Fig. 1A-B, E-H). The prefrontal-lacrimal contact is relatively straight and the prefrontal-frontal contact is irregular. The dorsal surfaces of the prefrontals are ornamented with a few medium-sized pits and grooves.

Lacrimals: The lacrimals are large, triangular shaped bones that can be seen in both dorsal and lateral views (Fig. A-B, E-H), similar to other teleosauroid taxa (e.g. *S. leedsi* NHMUK PV R 3806; *S. bollensis* SMNS 51563; *S. gracilirostris* NHMUK PV OR 14792; *Myc. nasutus* NHMUK PV R 2617). The lacrimal broadly contacts the nasal and constitutes the anterolateral border of the orbits and the anterior margin of the antorbital fenestra (Fig. 1A-B, E-H). The antorbital fenestrae are large, anteroposteriorly elongated and slightly oval-shaped (Fig. 1A-B, E-H), similar to those in *Steneosaurus gracilirostris* (NHMUK PV OR 14792) and differing from the small, subcircular antorbital fenestrae seen in other teleosauroids (e.g. *Myc. nasutus* NHMUK PV R 2617; *S. leedsi* NHMUK PV R 3806; the Chinese teleosauroid IVPP V 10098) (Fig. 11). The antorbital fenestrae are nearly a quarter of the anteroposterior orbital length (24%), similar to '*S.*' *brevior* (27%) (NHMUK PV OR 14781) and similar in design but not to the same extent as in *S. gracilirostris* (which is approximately 57%)

(NHMUK PV OR 14792). Other teleosauroids with antorbital fenestrae range from between 11% (e.g. *Myc. nasutus* NHMUK PV R 2617) and 16 % (e.g. *S. leedsi* NHMUK PV R 3806).

Frontal: The frontal (Fig. 1A-B) is a single, dorsoventrally deep bone with no evidence of a midline suture. The frontal forms a relatively straight vertical contact with the postorbital in dorsal and lateral views, forms the anterior medial borders of the supratemporal fenestrae and contributes to the posteromedial border of the orbits (Fig. 1A-B), which are large and sub-oval in shape. The anterior process is relatively long and slender, proceeding further anteriorly than the anterior margin of the orbits as in the majority of other teleosauroids (e.g. *S. leedsi* NHMUK PV R 3320; *S. edwardsi*, PETMG R178) but differing from *S. stephani* NHMUK PV OR 49126 (where the anterior process is relatively short and mediolaterally broad). The frontal dorsal surface is ornamented with pits that are restricted to the centre of the bone, and grooves that extend towards the lateral-most edges of the bone.

Postorbitals: Only the left postorbital is preserved (Fig. 1A-B, E-F). It is a broad, heavy bone, and reaches the orbit posteroventral margin, where it overlaps with the jugal. The postorbital forms the lateral and posteroventral margins of the supratemporal fenestra, as well as the posterior margin of the orbit, with the overall body being anteroposteriorly broadened (Fig. 1E-F). The postorbital bar (formed by the frontal-postorbital contact) is similar to other teleosauroids (e.g. *S. bollensis* SMNS 51753; *S. edwardsi* NHMUK PV R 3701; *L. obtusidens* LPP.M.21). It is slightly anteroposteriorly thickened and has small sparse pits for ornamentation in the medial part. The postorbital-squamosal contact is not preserved. While the specimen is broken into two pieces (see above) near the middle of the supratemporal fenestrae, they appear to be anteroposteriorly elongated and rectangular in shape (Fig. 1A-B).

Parietal: The single parietal is a relatively large, mediolaterally thickened bone (Fig. 1A-B), and has shallow dorsal ornamentation consisting of a few irregular pits. The anterior-most

end of the parietal is not preserved (Fig. 1A-B). The parietal contributes to the posterior and medial borders of the supratemporal fenestrae and does not overhang the occiput in dorsal view (Fig. 1I-J).

Squamosals: The majority of the squamosals (Fig. 1A-B) are not preserved; however, they are elongated L-shaped bones similar to those seen in other teleosauroids (e.g. *S. leedsi* NHMUK PV R 3806; *S. edwardsi* PETMG R178; *Mac. buffetauti* SMNS 91415). The anterior process is anteroposteriorly elongated (in dorsal view), and forms the posterolateral border of the supratemporal fenestrae. The posterolateral surface of the squamosal is concave in lateral view and convex in dorsal view (Fig. 1A-B). The squamosal bar is well-developed and contacts the postorbital bar anteriorly; together these two bones form the supratemporal arch, which is sparsely ornamented).

Quadrates: The quadrates (Fig. 1A-D, I-J) are of substantial size, and are strongly sutured to the squamosals and quadratojugals. The anterodorsal region of the quadrate contacts the squamosal and quadratojugal and medially contacts the exoccipital-opisthotic. Both hemicondyles are mediolaterally elongated (oval-shaped) with rounded posterior edges, as seen in other teleosauroids (e.g. *S. edwardsi* PETMG R178; *S. hebert*i MNHN.F 1890-13). The posteroventral medial hemicondyle is approximately the same in size and mediolateral length as the lateral hemicondyle, differing from *Mac. hugii* (MG-8730-1). On the occiput, the hemicondyles posteriorly extend slightly further than the exoccipital-opisthotic (Fig. 1I-J). The anterior-most quadrates are not preserved.

Quadratojugals: The posterior-most part of the quadratojugals is best preserved on the left side (Fig. 1C-D, I-J); the posterior region is expanded mediolaterally to accommodate the quadrate. Neither of the quadratojugals are visible in dorsal view.

Supraoccipital: The supraoccipital (Fig. 1I-J) is ventral to the parietal and only visible in occipital view. It is a single bone that forms the dorsomedial part of the occiput and contributes to the dorsal edge of the foramen magnum (Fig. 1I-J), as in all teleosauroids (e.g. *S. gracilirostris* MNHNL TU515; *S. leedsi* NHMUK PV R 3806; *S. heberti* MNHN.F 1890-13; *L. obtusidens* LPP.M.21). A moderate nuchal crest is present, smaller than that seen in *S. gracilirostris* (MNHNL TU515). The supraoccipital is dorsoventrally tall (although it is slightly dorsally crushed), mediolaterally expanded and slightly concave (Fig. 1I-J).

Exoccipital- opisthotics: The fused exoccipital-opisthotics (Fig. 1I-J) make up the majority of the occiput. They are tilted dorsally, flared mediolaterally and are slightly concave on their occipital surfaces. Both exoccipital-opisthoticss are directed posteriorly when seen in dorsal and occipital views. The exoccipital-opisthotics are mediolaterally elongated as in most other teleosauroids (e.g. *S. leedsi* NHMUK PV R 3806; *S. heberti* MNHN.F 1890-13), and contribute to the dorsal and lateral borders of the foramen magnum. The paraoccipital process is rounded and approximately the same size as the rest of the exoccipital, giving it a paddle-shaped appearance in occipital view (Fig. 1I-J). The foramen magnum is large and mediolaterally elongated (oval-shaped), as in other teleosauroids (e.g. *S. leedsi* NHMUK PV R 3806; *S. heberti* MNHN.F 1890-13; *Myc. nasutus* CAMSM J.1420). A foramen for cranial nerves XII is located on each side of the foramen magnum; these are large and positioned parallel to the foramen magnum (Fig. 1I-J) (see Brusatte et al., 2016). The distal part of the right exoccipital-opisthotic is not preserved.

Basioccipital: The basioccipital (Fig. 1C-D, I-J) forms the ventral part of the occiput. The basioccipital is slightly wider than tall and contributes to the foramen magnum. The occipital condyle is large and more circular than the foramen magnum (Fig. 1I-J), and is situated ventral to it. The basioccipital largely forms the occipital condyle. In ventral view, there are

two well-developed and slightly dorsoventrally elongated basioccipital tuberosities (Fig. 1C-D). These tuberosities slope slightly anteroventrally in occipital view (Fig. 2), similar to most teleosauroids (e.g. *S. leedsi* NHMUK PV R 3806; *S. edwardsi* PETMG R178; Machimosaurini) but smaller than those seen in *S. heberti* (MNHN.F 1890-13). There is a large, oval opening for cranial nerve XII (Fig. 1I-J) that is positioned laterally to the foramen magnum. There is also a very small subcircular foramen for cranial nerve IX that is ventrolaterally positioned to cranial nerve XII and parallel to the occipital condyle, seen on the left side of the basioccipital (Fig. 1I-J).

Basisphenoid: The basisphenoid (Fig. 1C-D) is relatively well preserved, although the anterior-most part is not preserved and the overall bone is slightly dorsoventrally crushed. The basisphenoid has two elongated posterolaterally directed processes and comes into posterior contact with the quadrate (Fig. 1C-D).

Pterygoid: The majority of the pterygoid, including the pterygoid wings, is not preserved (Fig. 1C-D). The anterior-most left and right pterygoids appear to be fused into one bone and thin, as in other teleosauroids (e.g. *S. leedsi* NHMUK PV R 3806; *S. bollensis* MNHNL TU799; *S. edwardsi* NHMUK PV R 2865; *Myc. nasutus* NHMUK PV R 2617), and contacts the posterior processes of the palatines.

Palatines: The paired palatines (Fig. 1C-D) are dorsoventrally thin, elongate bones and are similar to those seen in other teleosaurids, such as *S. leedsi* (NHMUK PV R 3806), *Myc. nasutus* (NHMUK PV R 2617), and the Chinese teleosauroid (IVPP V 10098). The palatines have a smooth, unaltered surface and are V- shaped (Fig. 1C-D). The posterior-most region of the left palatine is slightly distorted due to breakage, and there is a large, sub-horizontal crack filled with matrix across the middle of the palatines (see Fig. 1C-D). The anterior palatines have small anterior processes, which are slightly round and articulate with the posterior

process of the maxillae (Fig. 1C-D). These anterior processes reach approximately the 21st maxillary alveolar pair, which differs from machimosaurins (e.g. *Y. boutilieri* [OUMNH J.1403] terminates between the 15th and 19th maxillary alveolar pair, and *Mac. buffetauti* [SMNS 91415] terminates between the 11th and 14th maxillary alveolar pair). The palatines contact one another along the skull midline until they are posteriorly separated by the anterior process of the pterygoid. The suborbital fenestrae are poorly preserved and only the medial margin (formed by the palatine) of the left suborbital fenestra can be seen (Fig. 1C-D).

Other elements: The ectopterygoids, proötics and laterosphenoids, as well as other small bones of the braincase and palatal region, are not preserved and therefore unavailable for description.

Dentition: Twelve teeth are preserved; four of them are fully mature, and two are missing the apex (Fig. 1K). Of these teeth, two are from the premaxillae, three from the anterior maxillae, four from the middle maxillae and three from the posterior maxillae. The largest preserved tooth crown (left P3) is apicobasally 0.74 cm long (Fig. 1G-H, K). Throughout the dentition, the teeth (Fig. 1K) are large and robust but with a pointed apex, as opposed to the blunt apices seen in both *Lemmysuchus obtusidens* (e.g. NHMUK PV R 3168), *Yvridiosuchus boutilieri* (OUMNH J.29850) and *Machimosaurus* species (e.g. ONM 1-25; SMNS 91415). The four fully erupted teeth are posteriorly curved. The apicobasal enamel ridges are noticeable and well-developed, parallel to one another and reach the top of the apex (Fig. 1K). There is no mediolateral compression of the teeth (as opposed to *S. heberti* MHNH.F 1890-13) and there are very faint carinae visible all along the tooth crown. No characteristic machimosaurin anastomosing pattern is seen in the apices (Fig. 1K). Overall, the teeth of OUMNH J.29851 are similar in shape, size and ornamentation to those seen in large *S. edwardsi* specimens (e.g. PETMG R178).

Machimosaurini (Jouve et al., 2016)

Machimosaurini indeterminate (Fig. 2)

v 1995 *Steneosaurus larteti* (Deslongchamps); Vignaud, p. 188

We have examined two partial mandibles (OUMNH J.1406 and OUMNH J.1417) with in situ teeth that have the characteristic Machimosaurini dental pattern (which consists of blunt, conical teeth with a noticeable anastomosing pattern on all apices). The first partial mandible, OUMNH J.1406 (Fig. 6), is from the Great Oolite Group (Bathonian, Middle Jurassic) of North Oxfordshire and is part of the E.A. Walford collection. The anterior-most and posterior areas of the mandible are not preserved. The dentary is an elongate, slender bone that makes up the majority of the lower jaw in crocodylomorphs (Andrews, 1909, 1913; Romer, 1956; Nesbitt, 2011). It is difficult to determine where exactly the mandibular symphysis begins, as the dorsal surface of the dentary is poorly preserved, but it starts approximately at the 16th or 17th alveolus. There are at least 23 dentary alveoli preserved on the left side. The interalveolar spacing is variable throughout the dentary and the alveoli are subcircular in shape (Fig. 2A). In lateral view (Fig. 2A) there are deep reception pits throughout the entirety of the mandible, as well as a single line of large foramina running parallel to the tooth row. OUMNH J.1406 is well ornamented with pits and rugosities in lateral and ventral views (Figs. 2A). There is one partially erupted tooth preserved (Fig. 2A) in the 16th right alveolus. The tooth has a blunt, conical apex with the characteristic anastomosing pattern, and high relief enamel ridges.

The second mandible, OUMNH J.1417 (Fig. 2B), is relatively broad, with only the articulars, and posterior surangulars and angulars missing (more so on the right side than the left). As in OUMNH J.1406, the dentary is an elongate bone and make up the majority of the

mandible, with the mandibular symphysis beginning at the 16th alveolus (Fig. 2B). There are 29 alveoli preserved, and the posterior-most alveoli are only slightly smaller than those positioned in the anterior and middle sections of the dentary (Fig. 2B). All alveoli are subcircular in shape with interalveolar spacing varying throughout. The Meckelian groove of OUMNH J.1417 is deep, which differs from other Machimosaurini (e.g. *L. obtusidens* LPP.M.21; *Mac. buffetauti* SMNS 91415). In left lateral view, the surangular is a thin, anteroposteriorly elongated bone. There are deep reception pits present along the lateral margins of the entirety of the mandible, as well as a single line of large foramina running parallel to the tooth row (Fig. 2B). There are numerous large subcircular fenestrae in dorsal, lateral and ventral views in the anterior-most part of the dentary (Fig. 2B), arranged in a semi-circular pattern around the D1 to D4 alveoli. There are five partially erupted teeth (third left alveolus and second, 16th, 18th and 22nd right alveoli) (Fig. 2B). All teeth are robust with a blunt apex, and all preserve the characteristic anastomosing pattern.

Yvridiosuchus **Gen Nov.**

(Figs. 3-5)

Type species: *Teleosaurus boutilieri* Eudes-Deslongchamps, 1868 [following recommendation 67B of the ICZN Code]. Now referred to as *Yvridiosuchus boutilieri* (Eudes-Deslongchamps, 1868) comb. nov.

Diagnosis: same as the only known species (monotypic genus).

Etymology: "Hybrid crocodile". *Yvrídio* (υβρίδιο) is Ancient Greek for 'hybrid' (referring to unique combination of machimosaurin synapomorphies and non-machimosaurin teleosauroid

symplesiomorphies present in this genus), and *suchus* is the Latinized form of the Greek *soukhos* (σοῦχος), meaning crocodile

Yvridiosuchus boutilieri

Comb. Nov.

v 1821	Partial crocodile skull; Conybeare in: de la Bêche & Conybeare, p.591
v 1822	Partial crocodile skull; Conybeare; Conybeare & Phillips, p.208
v 1868a*	*Teleosaurus boutilieri* n. sp.; J.A. E-Deslongchamps, p.112-118, pl.5 fig.1-6
v 1868b	*Teleosaurus boutilieri* (Deslongchamps); J.A. E-Deslonchamps, p.121-129, pl.5, fig.8-10
v 1867-69	*Steneosaurus boutilieri* (Deslongchamps); E. Deslongchamps, p.228, pl.16, fig.1-2
v 1870a	*Steneosaurus boutilieri* (Deslongchamps); E. Deslongchamps, p.329
vp 1871	*Teleosaurus brevidens* n. sp.; Phillips, p.185-187, fig.44.1
v 1936	*Steneosaurus boutilieri* (Deslongchamps); Kuhn, p.38
v 1951	*Steneosaurus boutilieri* (Deslongchamps); Phizackerley, p.1177, fig. 4-6
v 1973	*Steneosaurus boutilieri* (Deslongchamps); Steel, p.31
(?) 1981	*Steneosaurus* sp.; Rieppel, p.739, fig.2

v 1995 *Steneosaurus boutilieri* (Deslongchamps); Vignaud, p.186-187, pl.2 fig.a-b

v 1996 *Steneosaurus boutilieri* (Deslongchamps); Godefroit et al., p.98

1998 *Steneosaurus boutilieri* (Deslongchamps); Mazin et al.

v 1998 *Steneosaurus boutilieri* (Deslongchamps); Vignaud, p.22

Holotype: A skull fragment figured by Eudes-Deslongchamps (1867-69), presumed to be lost or destroyed (Vignaud, 1995).

Holotype locality and horizon: "*Sommet de la Grande Oolithe*", Calvados, France.

Neotype: OUMNH J.1401, comprising an incomplete skull, with areas posterior to the orbits missing.

Designation of neotype: Herein we formally designate OUMNH J.29851 as the neotype of *Yvridiosuchus boutilieri*. In order to be in full accordance of Article 75 of the ICZN Code, in particular Article 75.3, we make the following statements:

1. This designation is made with the express purpose of clarifying the taxonomic status of *Yvridiosuchus boutilieri*.

2. Our statement of the characters that we regard as differentiating *Yvridiosuchus boutilieri* from other taxa is given by the species diagnosis below.

3. The neotype can be recognised through both the description below and Fig. 3.

4. The holotype is presumed destroyed in 1944 during the bombing of Caen.

5. The holotype had a partial skull; the description and figure given by E. Eudes-Deslongchamps (1868) showed it to be large, rugose and robust with broad, rounded palatines and robust teeth. As such, the neotype is consistent with what is known of the former name-bearing type.

6. Unfortunately, the neotype is not from the same locality or country as the holotype. However, E. Eudes-Deslongchamps compared the holotype with our proposed neotype, and considered that they were from the same species and included both in his future description of the species. In addition, both the holotype and our proposed neotype come from the equivalent to the Great Oolite Group in England.
7. The neotype is the property of a recognized scientific institution, OUMNH, which maintains a research collection with proper facilities for preserving name-bearing types, and is accessible for study.

Neotype locality and horizon: Cornbrash Formation, Great Oolite Group, Enslow Bridge, UK. Bathonian, Middle Jurassic.
Referred specimens: OUMNH J.29580, a complete skull and mandible (type specimen of *Teleosaurus brevidens* and *Steneosaurus meretrix*). OUMNH J.1403, a nearly complete skull. OUMNH J.1404, a partial mandible.

Etymology: "Boutilier's hybrid crocodile". 'υβρίδιο (yvrídio)' is Ancient Greek for 'hybrid', and 'σοῦχος (soûkhos)' is Ancient Greek for crocodile. Named after Mr. Boutilier, who gave the type specimen to Eugène Eudes-Deslongchamps.

Emended diagnosis: Teleosauroid crocodylomorph with the following unique combination of characters among teleosauroids [autapomorphic characters indicated by an asterisk (*)]: mesorostrine skull (rostrum less than 68% of total skull length) (shared with '*Steneosaurus*' *brevior*, the Chinese teleosauroid IVPP V 10098, *Deslongchampsina larteti*, *Steneosaurus edwardsi* and Machimosaurini); skull ornamented with conspicuous pits and grooves; heavily ornamented prefrontal and lacrimal (shared with '*S.*' *brevior* and *Mycterosuchus nasutus*); large and numerous neurovascular foramina on the premaxillae, maxillae and dentaries

(shared with '*S.*' *brevior* and Machimosaurini); external nares oriented dorsally (shared with *Steneosaurus gracilirostris*, *Steneosaurus bollensis*, *Steneosaurus leedsi, Steneosaurus heberti*, *D. larteti*, *S. edwardsi* and Machimosaurini);presence of antorbital fenestrae; frontal width subequal with orbital width (shared with the Chinese teleosauroid IVPP V 10098, *Myc. nasutus*, *S. heberti*, *D. larteti*, *Machimosaurus hugii*, and *Machimosaurus rex*); squamosal projects further posteriorly than occipital condyle (shared with the Chinese teleosauroid IVPP V 10098, *S. edwardsi* and Machimosaurini); orbit subcircular in shape (similar to other members of Machimosaurini); anterior process shape of palatine U-shaped*; Meckelian canal (=groove) is not deeply excavated on the dorsal surface of the splenials (shared with *S. heberti*, *S. edwardsi*, *L. obtusidens* and *Machimosaurus*); sharp dorsoposterior curvature of the posterior mandibular rami (shared with *S. heberti* and Machimosaurini); width of mid-retroarticular process is substantially narrower than the glenoid fossa*; teeth with no mediolateral compression (shared with *B. megarhinus*, *D. larteti*, *S. edwardsi*, and Machimosaurini); maxillary teeth not procumbent (shared with *S. heberti*, *S. edwardsi* and Machimosaurini).

Description

The neotype of *Y. boutilieri* (OUMNH J.1401) (Fig. 3) is a partial rostrum, preserved from the anterior-most part of the snout until the anterior margin of the supratemporal fenestrae. OUMNH J.1401 is broken into two sections (Fig. 3): the first piece is complete from the anterior margin to the right M15 and left M18 alveoli (a posteriorly-directed horizontal break), and the second piece includes the right M15 alveolus back to the supratemporal fenestra anterior margin. One area of the rostrum (including the right fourth premaxillary alveolus and the first four maxillary alveoli on both sides) is reconstructed with plaster (see Fig. 8). Two referred specimens, OUMNH J.28950 (Fig. 4) and OUMNH J.1403 (Fig. 5A-F),

represent additional skull material, including the palate (OUMNH J.1403) and the majority of the mandible (OUMNH J.29850). The premaxillary bones are not preserved in OUMNH J.1403, and the skull of OUMNH J.29850 is cemented to the mandible so that the palatal surface is not visible. In addition, OUMNH J.1404 (Fig. 5G-H), a partial mandible, has been referred to as '*S*'. *boutilieri* so we describe it here as well (however, it is unknown who referred this specimen to the species *boutilieri*, or when they did so).

Cranium: The crania of all aforementioned *Y. boutilieri specimens* (OUMNH J.1401, OUMNH, J. 28950, OUMNH J.1403) are massive and rugose (Figs. 3, 4, 5A-F), and are heavily ornamented with multiple deep, circular foramina, particularly around the premaxillae and anterior maxillae (see Description). The orbits are subcircular (Figs. 3A-B, E-H; 4A-B, E-H; 5A-B) and are slightly more anteroposteriorly elongated than other members of Machimosaurini (e.g. *L. obtusidens* LPP.M.21; *Mac. buffetauti* SMNS 91415; *Mac. mosae* IRSNB cast). In both OUMNH J.29850 and OUMNH J.1403, the supratemporal fenestrae are parallelogram-shaped (Figs. 4A-B, 5A-B). The entire cranium of OUMNH J.29850 measures approximately 78 cm from the anterior-most premaxillae to the posterior-most quadrates, and the quadrate-to-quadrate length is approximately 21 cm.

Premaxillae: The premaxillae (Figs. 3-4) are robust and surround the external narial opening. The external nares face dorsally, are laterally expanded and their posterior margins do not reach beyond the third premaxillary alveolar pair. The anterior two-thirds of the premaxilla is slightly laterally expanded and anteroposteriorly shortened, and the anterior margin is ventrally deflected. In dorsal view, the premaxilla-maxilla suture is subcircular in shape and slightly interdigitating (Fig. 3A-B, 4A-B). The incisive foramen (=naso-oral fenestra) is very small and is situated in the middle of the suture of the premaxillae. In OUMNH J.1401, four premaxillary alveoli are present (Fig. 3C-D). While the mandible of OUMNH J.29850 (Fig.

10) obscures the majority of the premaxillae of the ventral view, the lateral margins of four alveoli are also visible. The first two premaxillary alveoli are nearly confluent, with a thin interalveolar lamina separating them. The third and fourth premaxillary alveoli are well-separated (Fig. 3C-D) (see Foffa et al., in press). Both premaxillae are strongly ornamented with conspicuous pits and grooves (Figs. 3-4), and in dorsal and lateral views there is a clustering of large circular foramina along the anterior and lateral margins of the external nares (Figs. 3E-H, 4E-H).

Maxillae: The maxillae (Figs. 3A-G, 4A-G, 5A-D) form a substantial part of the rostrum. The elongated maxillae are transversely narrow and anteriorly separated by the premaxillae (Figs. 3A-G, 4A-G, 5A-D). In dorsal view, the maxillary lateral margins are sub-parallel, and the premaxillae and nasals are separated by the maxillae. In OUMNH J.1401, there are at least 26 maxillary alveolar pairs; in OUMNH J.29850, there are at least 25; and in OUMNH J.1403, there are at least 23 (with the anterior-most maxillae not being preserved). The reception pits are deep throughout the entirety of the maxilla, which is ornamented with well-developed pits and grooves. In addition, there are numerous, deep, well-spaced foramina (arranged in two lines parallel to the maxillary ventral margin) that are best visible in lateral views (Figs. 3A-B, E-H; 4A-B, E-H).

Jugals: The jugals (Figs. 3G-H, 4E-H, 5A-B) are triradiate, forming the lateral border of the orbit as in other teleosauroids (e.g. *S. leedsi* NHMUK PV R 3806; the Chinese teleosauroid IVPP V 10098; *S. heberti* MNHN.F 1890-13). In OUMNH J.1401, the anterior jugal is somewhat difficult to see but is better preserved on the left side and appears to extend anteriorly past the orbits (Fig. 3G-H). In OUMNH J.29850, the jugals also extend anteriorly past the orbits (Figs. 4E-H). The jugal participates in the ventral margin of the orbit, and the

postorbital-jugal contact (best seen in right lateral view) appears to be anteroposteriorly straight. The quadratojugal-jugal contact is not preserved in any specimen.

Nasals: The nasals (Figs. 3A-B, E-H; 4A-B, E-H; 5A-B) are large triangular bones exposed on the dorsal surface of the posterior rostrum and orbital area. The lateral margins of the nasals are strongly confluent, and the anterior area is mediolaterally narrow as in other teleosauroids (e.g. *S. leedsi* NHMUK PV R 3806; *D. larteti* OUMNH J.19851; *S. edwardsi* NHMUK PV R 2865). In OUMNH J.29850, it is difficult to describe the anterior-most nasals, as there is some slight discoloration in that particular area of the skull (Fig. 4A-B). The nasal anterior processes have a near-parallel sutural contact with the maxillae. In OUMNH. J.1401, OUMNH J.1403, and OUMNH J.29850, there is no dorsoventral 'doming' of the nasals and there is a faint internarial suture, suggesting that the nasals are unfused (both features differ from *L. obtusidens* specimens NHMUK PV R 3168, PETMG R39, LPP.M.21, NOTNH FS336, in which there is a dorsoventral 'dome' in the posterior nasals and no internarial suture is present).

Prefrontals: The prefrontals (Figs. 3A-B, E-H; 4A-B, E-H; 5A-B) are sub-circular shaped and longer than wide in dorsal view. The prefrontal forms the anteromedial border of the orbits, and contacts the nasal and frontal medially and the lacrimal laterally (Figs. 3A-B, E-H; 4A-B, E-H, 5A-B). The prefrontal-frontal contact is irregular and the prefrontal-lacrimal contact is relatively straight. In OUMNH J.1401, the prefrontal is ornamented with small and grooves, similar to those seen in *S. bollensis* (e.g. SMNS 51563, SMNS 51555, SMNS 59736).

Lacrimals: The lacrimals (Figs. 3A-B, E-H; 4A-B, E-H; 5A-B) are substantially sized triangular bones that constitute the majority of the anterolateral margins of the orbits, and can be observed in both dorsal and lateral views (Figs. 3A-B, E-H; 4A-B, E-H; 5A-B). The

lacrimals are well ornamented with small pits and grooves (similar to *Myc*. *nasutus* [NHMUK PV R 2617] and '*S*.' *brevior* [NHMUK PV OR 14781], but not as heavily ornamented as those two taxa). The paired antorbital fenestrae are small and anteroposteriorly elongated (Figs. 3A-B, E-H; 4A-B, E-H; 5A-B), with the right being better preserved than the left in OUMNH J.29850.

Frontal: In OUMNH J.1401, OUMNH J.1403 and OUMNH J.29850, the frontal (Figs. 3A-B, E-H; 4A-B, E-H; 5A-B) is a dorsoventrally deep bone, and there is no evidence of a midline suture. The frontal contributes to the posteromedial border of the orbits, forms a relatively straight vertical contact with the postorbital in dorsal and lateral views and forms the anterior medial borders of the supratemporal fenestrae (Figs. 3A-B, E-H; 4A-B, E-H; 5A-B). The anterior process is longer than other machimosaurins (e.g. *L*. *obtusidens* NHMUK PV R 3168), with the length being similar to *S*. *stephani* (NHMUK PV OR 49126). The frontal is ornamented with pits and grooves that are restricted to the centre of the bone. In OUMNH J.1403, the posterior frontal contacts the parietal (Fig. 5A-B).

Postorbitals: The postorbitals (Figs. 3A-B, E-H; 4A-B, E-H; 5A-B), best preserved in OUMNH J.19850 and OUMNH J.1403, reach the orbit posteroventral margin (with the postorbital overlapping the jugal), and extensively form parts of the orbit ventral margins (similar to *Platysuchus multiscrobiculatus* SMNS 9930). The postorbital also forms the lateral and posteroventral margins of the supratemporal fenestra (Figs. 4A-B, E-H; 5A-B). The anterodorsal suture interdigitates tightly with the frontal and forms the posterior margin of the orbit. In OUMNH J.29850 and OUMNH J.1403, the postorbital is noticeably larger and more elongate than the squamosal, and the postorbital-squamosal contact is straight (best seen in lateral view) (Fig. 4E-F). The anterodorsal area of the postorbital is slightly anteroposteriorly constricted (Figs. 4A-B, E-H; 5A-B), whereas the rest of it is

anteroposteriorly broad. The postorbital bar (formed by the frontal-postorbital contact) is similar to other teleosauroids (e.g. *S. bollensis* SMNS 51753; *S. edwardsi* PETMG R178; *D. larteti* OUMNH J.29851; *L. obtusidens* LPP.M.21), being slightly anteroposteriorly thickened, having small sparse pits for ornamentation and forming the posterolateral margin of the orbit.

Parietal: The parietal (Figs. 4A-B, E-H; 5A-B) is a relatively large and mediolaterally thickened single bone with no trace of a midline suture, with dorsal ornamentation that consists of two or three elliptical pits. The parietal contributes to the posterior and medial borders of the supratemporal fenestrae and does not overhang the occiput in dorsal view. The parietal bar is relatively thin, anteroposteriorly elongated and the posterior region is anteriorly concave.

Squamosals: The squamosals (Figs. 4A-B, E-H; 5A-B) are elongate L-shaped bones. The anterior process is anteroposteriorly elongated (in dorsal view), and forms the posterolateral border of the supratemporal fenestrae. The posterolateral surface of the squamosal is concave in lateral view and convex in dorsal view (Figs. 4A-B, E-H; 5A-B). The squamosal bar is robust and anteriorly contacts the postorbital bar (together forming the supratemporal arch).

Quadrates: In OUMNH J.29850, only the left quadrate (Fig. 4E-F) is well preserved and strongly sutured to the squamosal and quadratojugal. The anterodorsal region of the quadrate contacts the squamosal and quadratojugal while the posteroventral margin articulates with the articular (=jaw joint) and medially contacts the exoccipital-opisthotic. Both hemicondyles are similar in size (as seen in most other teleosauroids such as *S. bollensis* SMNS 59736; *L. obtusidens* NHMUK PV R 3168, but differing in *Machimosaurus* [e.g. *Mac. buffetauti* SMNS 91415; *Mac. mosae* IRSNB cast]), oval-shaped, mediolaterally elongate, and have

rounded posterior edges. On the occiput, the hemicondyles extend slightly more posteriorly than the exoccipital-opisthotics (Fig. 4I-J, 5E-F).

Quadratojugals: Only the left posterior-most quadratojugal is preserved in OUMNH J.29850 (Fig. 4A-B), with the posterior region being mediolaterally expanded to accommodate the quadrate.

Ectopterygoids: In OUMNH J.1403, the ectopterygoids are short and broad (Fig. 5C-D) and similar to other teleosauroids (e.g. *S. leedsi* NHMUK PV R 3320; *Myc. nasutus* NHMUK PV R 2617). The ectopterygoid contacts the maxilla anteriorly and the pterygoid posteriorly , and the ventral surface is slightly concave and curves ventromedially (Fig. 5C-D).

Supraoccipital: In OUMNH J.29850 and OUMNH J.1403, the supraoccipital (Figs. 4I-J, 5E-F) is positioned ventral to the parietal and is only visible in occipital view. It forms the dorsomedial part of the occiput and contributes to the dorsal margin of the foramen magnum (Figs. 4I-J, 5E-F). The ventral edge is triangular and there is no evidence of a pronounced nuchal crest, differing from *S. gracilirostris* (MNHNL TU515) and *L. obtusidens* (NHMUK PV R 3168). The supraoccipital is dorsoventrally tall, slightly mediolaterally expanded (more so dorsally than ventrally), not broadly exposed in dorsal view and slightly concave in occipital view.

Exoccipital-opisthotics: In OUMNH J.29850 and OUMNH J.1403, the exoccipital-opisthotics (Figs. 4I-J, 5E-F) make up the majority of the occiput. In OUMNH J.1403, the right exoccipital-opisthotic is not preserved and the anterior part of the left is missing. They are tilted dorsally, flared mediolaterally and are slightly concave on their occipital surfaces. Both exoccipital-opisthotics are strongly directed posteriorly, dorsoventrally tall and mediolaterally short compared to other non-machimosaurin teleosauroids (e.g. *S. leedsi*

NHMUK PV R 3806, *S. edwardsi* NHMUK PV R 3701; *S. heberti* MNHN.F 1890-13), and contribute to the dorsal and lateral borders of the foramen magnum. The paraoccipital process is rounded and the same size as the rest of the exoccipital-opisthotic, giving it a paddle-shaped appearance in occipital view (Figs. 4I-J, 5E-F). The foramina for cranial nerves XII are large, situated lateral to and on the same plane as the foramen magnum, and are housed in an oval-shaped fossa (Figs. 4I-J, 5E-F) similar to other teleosauroids (e.g. *S. heberti* MNHN.F 1890-13; *Steneosaurus baroni* Newton, 1893, NHMUK PV R 1999; *L. obtusidens* LPP.M.21).

Basioccipital: The basioccipital (Figs. 4I-J, 5E-F) forms the ventral part of the occiput. The basioccipital contributes to the ventral margin of the foramen magnum and is slightly wider than tall. The occipital condyle is larger and more circular than the foramen magnum (Figs. 4I-J, 5E-F). The sutures between the occipital condyle and the basioccipital are not visible. In OUMNH J.29850, there is a small circular foramen ventrolateral to cranial nerve XII and on the same plane as the occipital condyle on the left side of the basioccipital; this could possibly be the opening for cranial nerve IX (see Brusatte et al., 2016). Also in OUMNH J.29850, another large, circular foramen is situated lateral to the foramen magnum and ventral to the proximal paroccipital process. This opening is interpreted as either the vagus nerve (cranial nerve X) or a combination of the vagus, accessory (cranial nerve XI), and possibly glossopharyngeal (cranial nerve IX) (see Brusatte et al. 2016). The basioccipital tuberosities are slightly enlarged relative to most other teleosauroids, as in other members of Machimosaurini (e.g. *L. obtusidens* LPP.M.21; *Mac. mosae* [Hua, 1999; Young et al., 2014a]; *Mac. hugii* MG-8730-1), but smaller than those seen in *S. heberti* (MNHN.F 1890-13).

Basisphenoid: In both OUMNH J.1403 and OUMNH J.29850, the basisphenoid (Figs. 4IC-D, 5EC-D) has two elongated posterolaterally directed processes and comes into posterior contact with the quadrate. It is anteroposteriorly short and contacts the pterygoid anteriorly. In OUMNH J.1403, the basisphenoid is exposed along the palatal surface anterior to the quadrates and bifurcates the posterior part of the single pterygoid (Fig. 5C-D).

Pterygoid: In ventral view, the single fused pterygoid is well preserved in OUMNH J.1403 (Fig. 5C-D), as well as on the right side in OUMNH J.29850 (Fig. 4C-D). The pterygoid is anteroposteriorly elongated and mediolaterally expanded; it is also slightly dorsoventrally thick in comparison with other teleosauroids (e.g. *S. leedsi* NHMUK PV R 3806; the Chinese teleosauroid IVPP V 10098). The anterior pterygoid process articulates with the palatines. The pterygoid is concave and posterodorsally curved, most notably in the posterior area (Fig. 4C-D, 5C-D), and contributes to the medial and posterior borders of the sub-orbital fenestrae, which are tear-shaped (rounded posteriorly, thin and 'V'-shaped anteriorly and mediolaterally wide). The sub-orbital fenestrae are partially preserved in OUMNH J.1401 (Fig. 3C-D) and are slightly broken around the lateral margins; however, they are relatively well preserved in OUMNH J.1403 (especially the left suborbital fenestra) (Fig. C-D).

Palatines: The paired palatines (Fig. 3C-D, 5C-D) are dorsoventrally thin, elongate bones and are similar to those seen in other teleosaurids (such as *D. larteti* OUMNH J.29581; *S. leedsi* NHMUK PV R 3320; the Chinese teleosauroid IVPP V 10098). In both OUMNH J.1401 and OUMNH J.1403, the palatines have a smooth, unaltered surface and are relatively U-shaped (Figs. 3C-D, 5C-D). The anterior palatines are rounded, with a relatively small anterior processes (best seen in OUMNH J.1403) and articulate with the posterior processes of the maxillae (Figs. 5C-D). The palatines contact one another along the skull midline until they are posteriorly separated by the anterior process of the pterygoid. In OUMNH J.29850,

the posterior palatines strongly contact the pterygoid (Fig. 4C-D), slightly overlapping it. In OUMNH J.1401, the palatines reach the 19th or 20th maxillary alveolar pairs, which is similarly seen in other teleosauroid taxa (e.g. *D. larteti* OUMNH J.29851).

Other elements: In all specimens, the proötics are not visible and the laterosphenoids are poorly preserved; we were therefore unable to describe these bones properly.

Mandible: The nearly complete mandible of OUMNH J.29580 (Fig. 4A-H) is cemented to the cranium so the dorsal surface is not visible, as mentioned above. It measures approximately 74 cm in length; however, the posterior-most part of the mandible is not preserved. In OUMNH J.1404, the dorsal surface of the partially complete mandible is exposed (Fig. 5G-H), with the posterior portion not preserved.

Dentary: In both OUMNH J.29850 and OUMNH J.1404, the dentary (Figs. 4A-H, 5G-H) is an elongate, slim bone making up most of the lateral and ventral surfaces of the mandible (e.g. Andrews, 1909, 1913; Romer, 1956; Nesbitt, 2011). In OUMNH J.1404, the Meckelian groove is shallow and not deeply excavated on the dorsal surface of the splenials (Fig. 5G-H), which is also seen in *S. heberti* (MNHN.F 1890-13), *S. edwardsi* (NHMUK PV R 3701), *L. obtusidens* (LPP.M.21) and *Machimosaurus* (e.g. SMNS 91415). In dorsal view, the coronoid groove (best seen on the left side) is mediolaterally thick and penetrates deeply into the dentary (Fig. 5G-H). In OUMNH J.29850, the exact number of alveoli is difficult to discern but there are at least 29 alveoli per side (although the anterior-most dentary is missing); in OUMNH J.1404, there are at least 29 alveoli on the left side and 31-32 on the right (Fig. 5G-H). The alveoli are large and circular, with the interalveolar distance being slightly larger than the alveolar labiolingual width (Fig. 5G-H), and the interalveolar spacing ranges from large to small throughout the entirety of the mandible. In OUMNH J.1404, the posterior-most alveoli are approximately the same size as the anterior- and middle-situated alveoli (Fig. 5G-

H), which differs from other teleosauroids (e.g. *S. leedsi* NHMUK PV R 3806; *S. edwardsi* NHMUK PV R 3701; *Myc. nasutus* NHMUK PV R 2617; *Aeolodon priscus* von Sömmerring, 1814, NHMUK PV R 1806; *L. obtusidens* LPP.M.21) and is similar to *S. heberti* (MNHN.F 1890-13).

Surangular and angular: In both OUMNH J.29850 and OUMNH J.1404, the surangular (Figs. 4A-H, 5G-H) is a thin and anteroposteriorly elongate bone in lateral view, and in conjunction with the angular and articular forms a distinctive 'V' shape. In OUMNH J.1404, the anterior surangular terminates near the final alveolus of the dentary. In OUMNH J.29850, the angular (Fig. 4A-H) occupies a larger area than the surangular and is ventral to it. The angular is dorsoventrally deeper and more robust than the surangular and has a poor dorsal curvature in lateral view, similar to other teleosauroids (e.g. *S. leedsi* NHMUK PV R 3806; *S. edwardsi* NHMUK PV R 3701). In OUMNH J.29850, the left mandibular fenestra is anteroposteriorly elongated and dorsoventrally thin (Fig. 4E-F).

Articular: In OUMNH J.29850, the left articular is not preserved; however, the right articular is a separated piece from the mandible (Fig. 4K). In lateral view, the posterior mandibular rami is sharply curved dorsoposteriorly, similar to *S. heberti* (MNHN.F 1890-13) and Machimosaurini. The retroarticular process is anteroposteriorly elongate, mediolaterally thin and triangular-shaped in dorsal view (Fig. 4K). The anteroposterior keel is small and thin but visible, and the posterior end of the retroarticular process is slightly rounded. The middle area of the retroarticular process is substantially narrower than the glenoid fossa (39%), as opposed to other teleosauroids (e.g. 55% in *S. edwardsi* PETMG R178; 53% in *S. leedsi* NHMUK PV R 3320; 65% in *S. heberti* MNHN.F 1890-13).

Dentition: Throughout the dentition, the teeth (Fig. 4L) of *Yvridiosuchus boutilieri* are large and robust with a blunt apex, and are more similar to *Lemmysuchus* than *Machimosaurus*,

being slightly less conical and weakly curved in the anterior dentary. In OUMNH J.29850, the largest tooth (M14) measure approximately 1.5 cm in apicobasal length. The enamel ridges are small yet well-developed, parallel to one another and reach the top of the apex. The enamel is thinner towards the base of the crown and becomes progressively thicker towards the apex (Fig. 4L), similar to that seen in *Lemmysuchus* and *Machimosaurus* (Young & Steel, 2014; Johnson et al., 2017). There are numerous protruding apicobasal enamel ridges on the teeth, giving them a 'wrinkled' texture; these apicobasal ridges are close to one another and run parallel from the base of the crown to approximately three quarters of the entire tooth. At the apex, the ridges are considerably shorter and are organized in the typical anastomosed pattern that has been described for other members of Machimosaurini (*L. obtusidens* NHMUK PV R 3168; *Mac. buffetauti* SMNS 91415; *Mac. hugii* MG-8730-1; *Mac. rex* ONM 1-25; Young et al., 2014a, 2015a; Jouve et al., 2016; Johnson et al., 2017). The teeth have true denticles and false denticles (Young et al., 2015a), although the latter cannot be seen clearly with the naked eye.

Phylogenetic analysis

Methods. We conducted a phylogenetic analysis to test the evolutionary relationships of *Deslongchampsina larteti* gen nov. and *Yvridiosuchus boutilieri* gen. nov. within Thalattosuchia, using a modified version of the dataset provided by Foffa et al. (in press), which is based off of Ősi et al (2018). This dataset is continuously being updated, as it forms the foundation of the ongoing Crocodylomorph SuperMatrix Project. The dataset was first presented in Ristevski et al. (2018); however, it has been extensively updated subsequently (see Ősi et al. (2018) and Foffa et al. (in press) for full details). All data are summarised in Supplementary data files.

The current dataset consists of 143 crocodylomorph OTUs (70 of which are thalattosuchians, including 18 teleosauroids, seven basal metriorhynchoids and 42 metriorhynchids) scored for 464 characters. Of these 464 characters, 25 characters representing morphoclines were treated as ordered (see supplementary data). *Postosuchus kirkpatricki* Chatterjee, 1985 was used as the outgroup taxon. The differences between our analyses and those presented by Foffa et al. (in press) are: (1) the inclusion of a new taxon, *Yvridiosuchus boutilieri*; (2) the rescoring of *Deslongchampsina larteti*; (3) the re-scoring of '*Steneosaurus*' *brevior*; and (4) a re-organisation of the character list, with the addition of 8 new characters (Ch. 17-18, 176, 355, 362, 367, 374, 464). The character scorings for both *Y. boutilieri* and *D. larteti* were based on first-hand examination of the relevant material by MMJ; *D. larteti* was scored for 225 out of 464 characters (48.4%), and *Y. boutilieri* was scored for 292 out of 464 characters (62.9%).

The cladistic maximum parsimony analysis of the dataset was conducted using TNT 1.5 Willi Hennig Society Edition (Goloboff et al., 2008; Goloboff and Catalano, 2016), following the methodology used in Young et al. (2016). Memory settings were increased with General RAM set to 900 Mb and the maximum number of trees to be held set to 99,999. Cladogram space was searched by means of the 'New Technology search' option in TNT (Sectorial Search, Ratchet, Drift, and Tree fusing) with 1000 random-addition replicates (RAS). In addition, we increased the default setting for the iterations of each method (except for Tree fusing, which was kept at three rounds). In the Sectorial Search we ran 1000 Drift cycles (for selections of above 75) and 1000 starts and fuse trees 1000 times (for selections below 75), as well as 1000 rounds of Consensus Sectorial Searches (CSSs) and Exclusive Sectorial Searches (XSSs). For Ratchet, the program used 1000 ratchet iterations set to stop the perturbation when 1000 substitutions were made or 99% of the swapping was reached. Lastly, in Drift, the analysis included 1000 Drift cycles set to stop the perturbation when

1000 substitutions were made or 99% of the swapping was reached. The collapsing rule used was 50%. In addition to the strict unweighted consensus, we (1) analysed a majority rules unweighted consensus (cut-off 50%), and (2) ran the analysis once more using implied weighing (k = 12).

Results. The phylogenetic analysis produced 201 most parsimonious trees (MPTs) with 1526 steps (ensemble consistency index (CI) = 0.415; ensemble retention index (RI) = 0.845; ensemble rescaled consistency index (RCI) = 0.351; ensemble homoplasy index (HI) = 0.585) (Fig. 6A). The overall strict consensus topology recovered from this analysis is extremely similar to that presented by Ristevski et al. (2018), Ősi et al. (2018) and Foffa et al. (in press).

In the strict consensus tree (Fig. 6A), both *Deslongchampsina larteti* and *Yvridiosuchus boutilieri* were recovered in the teleosauroid subclade that includes typical '*Steneosaurus*' taxa (e.g. *Steneosaurus leedsi*) along with the durophagous tribe Machimosaurini (consisting of *Lemmysuchus* and *Machimosaurus*). *Yvridiosuchus boutilieri* is recovered in a polytomy with *Lemmysuchus obtusidens* and *Machimosaurus* taxa, but is clearly situated within the tribe Machimosaurini. *Deslongchampsina larteti* is recovered in an unresolved position with *Steneosaurus heberti*, and the clade containing *Steneosaurus edwardsi* and Machimosaurini (including *Y. boutilieri*). It is also interesting to note that *Steneosaurus gracilirostris*, currently considered the basal-most teleosauroid (see Ősi et al. 2018; Foffa et al. in review), forms an unresolved polytomy with *Steneosaurus bollensis*, '*Steneosaurus*' *brevior* and the Chinese teleosauroid (IVPP V 10098).

The majority rule consensus tree shows increased resolution (Fig. 6B). It places *Deslongchampsina larteti* as the sister taxon to the group containing *Steneosaurus heberti*, *Steneosaurus edwardsi* and Machimosaurini. The machimosaurin genera *Yvridiosuchus*,

Lemmysuchus and *Machimosaurus* continue to be in a trichotomy. *Steneosaurus gracilirostris* is positioned as the basal-most teleosauroid, as in Foffa et al. (in review).

Lastly, when the analysis was run once again using implied weighting (Fig. 6C): (1) *D. larteti* was recovered as the sister group to *Steneosaurus heberti* + *Steneosaurus edwardsi* + Machimosaurini; (2) *Yvridiosuchus boutilieri* came out within Machimosaurini (but again with the genera being in a trichotomy); and (3) *Steneosaurus gracilirostris* was the basal-most teleosauroid. The Chinese teleosauroid (IVPP V 10098) was placed as sister taxon to the grouping including '*Steneosaurus*' *brevior*, *Mycterosuchus nasutus*, *Aeolodon priscus* and *Bathysuchus megarhinus*.

Overall, the crocodylomorph interrelationships found in our analysis are similar to those recovered in previous iterations of this constantly growing dataset (Ristevski et al., 2018; Ősi et al., 2018; Foffa et al., in press; Sachs et al., in review). All phylogenetic analyses are similar concerning the following aspects:

1. The monophyly and positioning of Thalattosuchia within Crocodyliformes.
2. The separation of Thalattosuchia into two distinct clades: Teleosauroidea and Metriorhynchoidea.
3. The monophyly of Teleosauroidea.
4. Within Teleosauroidea, *Steneosaurus gracilirostris* is the likely basal-most species, with two subclades being recovered: (1) a group of poorly known taxa (e.g. *Platysuchus*, *Mycterosuchus*, *Aeolodon* and *Teleosaurus*) that are predominately longirostrine, and (2) the typical '*Steneosaurus*' group (e.g. *Steneosaurus leedsi*, *Steneosaurus edwardsi*), including the monophyletic tribe Machimosaurini (e.g. *Lemmysuchus* and *Machimosaurus*).

5. In Metriorhynchoidea, *Pelagosaurus typus* Bronn, 1841 is recovered as the basal-most metriorhynchoid, and the following groups are monophyletic: Metriorhynchidae, Metriorhynchinae, Rhacheosaurini, Geosaurinae and Geosaurini.

Discussion

1.1 Deslongchampsina larteti *compared to other teleosauroids*

Deslongchampsina larteti shares a number of characteristics with other teleosauroids, most notably with a handful of typical '*Steneosaurus*' taxa such as *Steneosaurus heberti* (MNHN.F 1890-13), *Steneosaurus leedsi* (NHMUK PV R 3806), and *Steneosaurus edwardsi* NHMUK PV R 3701, PETMG R178) (see Table 1). *Deslongchampsina larteti* (OUMNH J.29851), *S. heberti* (MNHN.F 1890-13), *S. leedsi* (NHMUK PV R 3806) and *S. edwardsi* (NHMUK PV R 3701, PETMG R178) differ from members of Machimosaurini (i.e. *Yvridiosuchus*, *Lemmysuchus* and *Machimosaurus*) in the following characters:

1. The cranium (e.g. *D. larteti* OUMNH J.29851) has a slightly proportionally longer snout (66%) than members of Machimosaurini such as *Y. boutilieri* (63%; OUMNH J.29850), *L. obtusidens* (61%) and *Mac. buffetauti* (59.6%; SMNS 91415, Young et al., 2014a);
2. There is a single parallel line of small neurovascular foramina on the lateral premaxillae, maxillae and dentaries. Taxa within Machimosaurini (e.g. *Y. boutilieri* OUMNH J.29850; *L. obtusidens* NHMUK PV R 3168; *Mac. buffetauti* SMNS 91415) have two lines of larger, irregularly shaped neurovascular foramina, as well as a

general clustering of foramina around the lateral margins of the external nares (Fig. 7);

3. The palatine anterior margin (e.g. *D. larteti* OUMNH J.29851; *S. leedsi* NHMUK PV R 3806) terminates posterior to the 20th maxillary alveoli. In Machimosaurini, the palatine anterior margin terminates either level to the 15th to 19th maxillary alveoli (e.g. *Y. boutilieri* OUMNH J.1403) or 11th to 14th maxillary alveoli (e.g. *Mac. buffetauti* SMNS 91415);
4. The supratemporal fenestrae are sub-rectangular in shape (e.g. *D. larteti* OUMNH J.29851; *S. leedsi* NHMUK PV R 3806), whereas in Machimosaurini (e.g. *Y. boutilieri* OUMNH J.29850; *L. obtusidens* NHMUK PV R 3168; *Mac. buffetauti* SMNS 91415; *Mac. mosae* IRSNB cast; Hua, 1999; Young et al., 2014a) they are parallelogram-shaped;
5. Reception pits are only visible in the anterior half of the maxillae (e.g. *D. larteti* OUMNH J.29851; *S. edwardsi* NHMUK PV R 3701; '*S.*' *brevior* NHMUK PV OR 14781; *S. heberti* MNHN.F 1890-13), whereas in Machimosaurini the reception pits are deep and visible until the posterior-most maxillae (e.g. *Y. boutilieri* OUMNH J.1401, OUMNH J.29850; *L. obtusidens* NHMUK PV R 3168, LPP.M.21; *Mac. buffetauti* SMNS 91415);
6. The teeth have pointed apices (e.g. *D. larteti* OUMNH J.29851; *S. heberti* MNHN.F 1890-13), whereas in Machimosaurini the apices are blunt and rounded (e.g. *Y. boutilieri* OUMNH J.29850; *L. obtusidens* NHMUK PV R 3168; *Mac. buffetauti* SMNS 91415; *Mac. mosae* [Hua, 1999]; *Mac. hugii* MG-8730-1; *Mac. rex* ONM NG 1-25) (Fig. 8);
7. The teeth have slight curvature throughout the entire dentition series (e.g. *D. larteti* OUMNH J.29851; *S. edwardsi* NHMUK PV R 3701), whereas in Machimosaurini

(e.g. *Y. boutilieri* OUMNH J.29850; *L. obtusidens* NHMUK PV R 3168; *Mac. buffetauti* SMNS 91415; *Mac. mosae* [Hua, 1999]; *Mac. hugii* MG-8730-1; *Mac. rex* ONM NG 1-25) at least the posterior teeth crowns are not curved (Fig. 8);

8. The teeth lack an apical macroscopic anastomosing enamel ornamentation pattern (e.g. *D. larteti* OUMNH J.29851; *S. edwardsi* PETMG R178; *S. heberti* MNHN.F 1890-13), whereas this pattern is present in all Machimosaurini teeth (e.g. *Y. boutilieri* OUMNH J.29850; *L. obtusidens* NHMUK PV R 3168; *Mac. buffetauti* SMNS 91415; *Mac. hugii* MG-8730-1; *Mac. rex* ONM NG 1-25) (Fig. 8).

In addition, *Deslongchampsina larteti* also shares one characteristic feature with *Steneosaurus edwardsi* (e.g. NHMUK PV R 2865, PETMG R178): robust, pointed teeth with no mediolateral compression (differing from most non-machimosaurin teleosauroids, e.g. *S. leedsi* NHMUK PV R 3806, *A. priscus* MNHN.F.CNJ 78; *S. heberti* MNHN.F 1890-13), and no anastomosing pattern (differing from Machimosaurini, e.g. *Y. boutilieri* OUMNH J.29850; *L. obtusidens* NHMUK PV R 3168; *Mac. buffetauti* SMNS 91415) (Fig. 8).

In the strict consensus topology (Fig. 14a), *D. larteti* is recovered in a polytomy with *S. heberti* (e.g. MNHN.F 1890-13) and the *S. edwardsi* + Machimosaurini clade. However, *D. larteti* differs from *S. heberti* (MNHN.F. 1890-13) in a number of features:

1. In *D. larteti* (OUMNH J.29851), the premaxillae are relatively dorsoventrally short and poorly constricted posteriorly, whereas in *S. heberti* (MNHN.F 1890-13) the premaxillae are dorsoventrally tall and posteriorly strongly constricted (Fig. 9);
2. In *D. larteti* (OUMNH J.29851), a midline cavity is present and the nasals gently slope anteroventrally, whereas in *S. heberti* (MNHN.F 1890-13) the cavity is absent, and the nasals are flat and do not slope ventroanteriorly;

3. In *D. larteti* (OUMNH J.29851), large antorbital fenestrae are present, whereas they are absent in *S. heberti* (MNHN.F 1890-13) (Fig. 10B-C);
4. The occipital tuberosities are smaller and more reduced in *D. larteti* (OUMNH J.29851), whereas in *S. heberti* (MNHN.F 1890-13) the tuberosities are large and bulbous; and
5. The teeth in *D. larteti* (OUMNH J.29851) are not mediolaterally compressed, while in *S. heberti* (MNHN.F 1890-13) they are (Fig. 8A-B).

Deslongchampsina larteti also shares one key character with *Steneosaurus gracilirostris* (NHMUK PV OR 14792): a pair of large, anteroposteriorly elongated antorbital fenestrae that are nearly half the diameter of the orbit (Fig. 18). This differs from other teleosauroids which either have smaller, subcircular antorbital fenestrae (e.g. *Y. boutilieri* OUMNH J.29850; *S. bollensis* SMNS 51753; *Myc. nasutus* NHMUK PV R 3577) or none at all (e.g. *S. heberti* MNHN.F 1890-13; *S. edwardsi* PETMG R178; *L. obtusidens* PETMG R39; *Mac. buffetauti* SMNS 91415) (Fig. 10).

1.2 Yvridiosuchus boutilieri *compared to other teleosauroids*

Yvridiosuchus boutilieri has a mosaic combination of characteristics, with some seen in Machimosaurini (most notably *Lemmysuchus*), and others in non-machimosaurin teleosauroids (e.g. '*S.*' *brevior* NHMUK PV OR 14781). Non-machimosaurin teleosauroid features seen in *Y. boutilieri* include:

1. The rostral height and width are subequal, similar to *L. obtusidens* (NHMUK PV R 3168) and all other non-machimosaurins (e.g. *S. heberti* MNHN.F 1890-13; *A.*

priscus MNHN.F.CNJ 78; the Chinese teleosauroid IVPP V 10098; *S. edwardsi* NHMUK PV R 2865);

2. There is an expanded network of neurovascular openings on the dorsal, lateral and ventral surfaces of the rostrum mandible, as in '*S.*' *brevior* (NHMUK PV OR 14781);
3. The antorbital fenestrae are present, as in *D. larteti* (OUMNH J.29851), *S. leedsi* (NHMUK PV R 3806), *S. bollensis* (SMNS 51753, 51957), *Myc. nasutus* (NHMUK PV R 3577, CAMSM J.1420), '*S.*' *brevior* (NHMUK PV OR 14781), the Chinese teleosauroid (IVPP V 10098), *P. multiscrobiculatus* (SMNS 9930) and *Teleosaurus cadomensis* Lamouroux, 1820 (MNHN AC 8746; Westphal 1962) (see Fig. 10); and
4. The frontal is subequal with orbital width, as in *D. larteti* (OUMNH J.29851), *S. heberti* (MNHN.F 1890-13), *Myc. nasutus* (NHMUK PV R 3577) and the Chinese teleosauroid (IVPP V 10098).

More importantly, *Yvridiosuchus boutilieri* (OUMNH J.1401, OUMNH J.29850) displays multiple features seen within Machimosaurini, and shares the following characters with *L. obtusidens* (NHMUK PV R 3168) that differ from *Machimosaurus* (i.e. *Machimosaurus* autapomorphies) (see Table 2):

1. There are four premaxillary alveolar pairs in *Y. boutilieri* (OUMNH J.1401) and *L. obtusidens* (NHMUK PV R 3168); *Machimosaurus* sp. have three premaxillary alveolar pairs (e.g. SMNS 91415; Young et al., 2014a);
2. There are 29 or more maxillary alveolar pairs in both *Y. boutilieri* (OUMNH J.29850) and *L. obtusidens* (NHMUK PV R 3168); *Mac. buffetauti* has approximately 21-28

maxillary alveolar pairs and *Mac. mosae* (Young et al., 2014a) has approximately 17-20 alveolar pairs;

3. There are at least 29 alveoli per dentary in *Y. boutilieri* (OUMNH J.29850) and *L. obtusidens* (NHMUK PV R 3168), whereas *Machimosaurus* sp. have approximately 19-25 alveoli per dentary;
4. All teeth have carinae in *Y. boutilieri* (OUMNH J.29850) and L. obtusidens (NHMUK PV R 3168), whereas the presence of carinae is variable in *Machimosaurus* sp.;
5. The rostrum is less mediolaterally broad in *Y. boutilieri* (OUMNH J.29850) and *L. obtusidens* (NHMUK PV R 3168) than in *Machimosaurus* sp. (e.g. *Mac. buffetauti* SMNS 91415; *Mac. mosae* IRSNB cast);
6. In *Y. boutilieri* (OUMNH J.29850) and *L. obtusidens* (NHMUK PV R 3168), the medial hemicondyle of the quadrate is smaller than the lateral hemicondyle, whereas in *Machimosaurus* sp. (e.g. *Mac. hugii* MG-8730-1) both condyles are approximately the same size.

Yvridiosuchus boutilieri has the following machimosaurin autapomorphies (seen in both *L. obtusidens* and *Machimosaurus* sp.):

1. Conical teeth with blunt/rounded apices (Fig. 8);
2. Tooth enamel varies along the crown (in the basal region enamel ornamentation is composed of numerous apicobasally aligned ridges of high relief, which transition into an anastomosed pattern in the apical region);
3. Teeth have both true and false denticles;
4. Anterior-middle teeth have no more than 85° or no curvature;
5. Pronounced socket-like reception pits along the entirety of the maxilla and dentaries (excluding the posterior-most areas) for the opposing tooth row;

6. Large neurovascular foramina present in two parallel lines along the lateral margins of the premaxillae, maxillae and dentaries (Fig. 7); and
7. Parallelogram-shaped supratemporal fenestrae in dorsal view.

While our phylogenetic analyses (Figs 6) does not resolve whether *Y. boutilieri* (OUMNH J.1401, OUMNH J.29850) and *L. obtusidens* (NHMUK PV R 3168) are sister taxa (or if one is more closely related to *Machimosaurus* than the other), these two taxa differ in a number of key characteristics:

1. The neurovascular foramina are very large, especially in the premaxillae, in *Y. boutilieri* (OUMNH J.1401, OUMNH J.29850), whereas in *L. obtusidens* (NHMUK PV R 3168, NOTNH FS3361) they are smaller. There is also a more disorganized clustering of the foramina across the premaxillae and around the lateral margins of the external nares in *Y. boutilieri* (OUMNH J.1401, OUMNH J.29850) (Fig. 16d-e);
2. Small anteroposteriorly elongated antorbital fenestrae are present in *Y. boutilieri* (OUMNH J.1401, OUMNH J.29850, OUMNH J.1403), whereas they are absent in *L. obtusidens* (NHMUK PV R 3168, LPP.M.21, PETMG R39) (Fig. 10C, E);
3. In *Y. boutilieri*, there is a small midline concavity present along the posterior nasals (best seen in OUMNH J.1401), whereas *L. obtusidens* (LPP.M.21, PETMG R39) this concavity is absent;
4. The orbit is slightly more anteroposteriorly elongate in *Y. boutilieri* (OUMNH J.1401, OUMNH J.1403, OUMNH J.29850), whereas they are circular in *L. obtusidens* (LPP.M.21, NHMUK PV R 3168);
5. The frontal width is subequal to the orbital width in *Y. boutilieri* (OUMNH J.1401, OUMNH J.29850), whereas in *L. obtusidens* (LPP.M.21) the frontal width is broader

(both *Mac*. *hugii* and *Mac*. *rex* [see Young et al., 2014a; Fanti et al., 2016] also share the same state as *Y*. *boutilieri*);

6. In *Y*. *boutilieri* (OUMNH J.1403), the anterior palatines are U-shaped, whereas in *L*. *obtusidens* (LPP.M.21) they are V-shaped;
7. In *Y*. *boutilieri* (OUMNH J.29850), the retroarticular process of the mandible is narrower than the glenoid fossa, whereas in *L*. *obtusidens* (NHMUK PV R 3168) the glenoid fossa is narrower than the retroarticular process;
8. In *Y*. *boutilieri* (OUMNH J.29850, OUMNH J.1403), the keeled carinae on the apex of the teeth are faint, as in *Mac*. *buffetauti* (SMNS 91415), *Mac*. *hugii* (MG-8730-1) and *Mac*. *rex* (OMN NG 1-25), whereas the teeth of *L*. *obtusidens* (NHMUK PV R 3168) have large, noticeably keeled carinae.

Currently, it is unclear whether *Y*. *boutilieri* or *L*. *obtusidens* is the sister taxon to *Machimosaurus*. The lack of post-cranial remains for *Y*. *boutilieri* is undoubtedly one of the primary reasons the three machimosaurin genera are recovered as a polytomy, especially given how apomorphic the post-cranial skeleton of machimosaurins are (see Young et al., 2014a; Johnson et al., 2017). As noted above, both *Y*. *boutilieri* and *L*. *obtusidens* lack numerous *Machimosaurus* autapomorphies; but both have some characters in common with *Machimosaurus* and not each other (see Table 2). This character conflict is interesting, as it hints that there could be more morphological variation in Machimosaurini than currently realised.

As mentioned previously, Hulke (1877) described and figured a new species, *Steneosaurus stephani* (NHMUK PV OR 49126) and compared it with '*D*.' *larteti* and '*Y*.' *boutilieri*, as well as *S*. *megistorhynchus*. While Vignaud (1995) listed this species as being synonymous with *Y*. *boutilieri*, NHMUK PV OR 49126 lacks the parallelogram-

shaped supratemporal fenestrae observed in all Machimosaurini (e.g. *Y. boutilieri* OUMNH J.29850; *L. obtusidens* NHMUK PV R 3168; *Mac. buffetauti* SMNS 91415; *Mac. mosae* IRSNB cast). *Steneosaurus stephani* (NHMUK PV OR 49126) also differs from *Y. boutilieri* (OUMNH J.29850) in having:

1. A very broad frontal with a small, mediolaterally broad anterior process (the frontal in *Y. boutilieri* [OUMNH J.29850] is more medially constricted and the anterior process is thin and elongated) (Fig. 11A-B);
2. A gentle dorsoposterior inclination of the retroarticular process (in *Y. boutilieri* [OUMNH J.29850] the retroarticular process is sharply dorsoposteriorly inclined);
3. Small postorbitals (these are much larger in *Y. boutilieri* [OUMNH J.1401, OUMNH J.29850]) (Fig. 11A-B); and
4. No evidence of antorbital fenestrae (small anteroposteriorly elongated antorbital fenestrae are present in *Y. boutilieri* [OUMNH J.1401, OUMNH J.29850]) (Fig. 11A-B), although this may be due to preservation.

In addition, NHMUK PV OR 49126 differs from *Deslongchampsina larteti* (OUMNH J.29851) in the following ways:

1. There is no evidence of antorbital fenestrae in NHMUK PV OR 49126, as opposed to the large, anteroposteriorly elongated antorbital fenestrae in *D. larteti* (OUMNH J.29851), although this may be a preservation issue (see above);
2. The anterior projection of the frontal is much shorter and broader in NHMUK PV OR 49126 than in *D. larteti* (OUMNH J.29851) (Fig. 11A, C);
3. NHMUK PV OR 49126 has circular orbits, whereas *D. larteti* (OUMNH J.29851) has oval-shaped orbits (Fig. 11A, C); and

4. NHMUK PV OR 49126 has relatively large basituberosities, as opposed to *D. larteti* (OUMNH J.29851) where the basituberosities are reduced.

Furthermore, neither the rostrum nor associated teeth are preserved in NHMUK PV OR 49126, so we cannot assess whether it has critical machimosaurin characters (e.g. large and numerous neurovascular foramina or blunt tooth crowns with anastomosed apical enamel ornamentation). Therefore, we currently agree with Hulke's (1877) diagnosis and provisionally retain NHMUK PV OR 49126 as a distinct taxon, *S. stephani*.

1.3 Bathonian teleosauroids of northern Africa

As mentioned previously, Jouve et al. (2016) described fragmentary indeterminate machimosaurin material (MHNM.I ss02) from Morocco. This material included a strongly abraded anterior portion of the dentary, with one in situ tooth. Four alveoli are preserved on the left side, and three alveoli on the right. The anterior dentaries' and tooth morphology in MHNM.I ss02 (e.g. blunt apex, anastomosing pattern, false denticles) is similar to that seen in all members of Machimosaurini (*Yvridiosuchus*, *Lemmysuchus* and *Machimosaurus*), but there are no distinguishing features that specifically refer it to *Yvridiosuchus* (e.g. OUMNH J.1404). Therefore, MHNM.I ss02 should currently remain as Machimosaurini indeterminate.

Jouve et al. (2016) also mentioned small fragments of Moroccan material (MHNM.I ss01) that he attributed to Teleosauroidea indeterminate. These include a small section of skull (including the maxilla, lacrimal and possible jugal) and posterior mandible (which includes eight alveoli and sections of the dentary and palatine). In the mandibular piece, in lateral view, there appears to be very slight reception pits, which are

seen in the posterior part of the dentary in *Y. boutilieri* (e.g. OUMNG J.29850); however, as there is currently no substantial mandibular material referred to *Deslongchampsina* it is difficult to make a comparison. Jouve et al. (2016) suggested that MHNM.I ss01 might belong to a longirostrine, narrow-snouted taxon, which would tentatively suggest *Deslongchampsina* (e.g. OUMNH J.29851) rather than *Yvridiosuchus* (e.g. OUMNH J.1401). However, this material is much too fragmentary, in particular the skull fragment, to confidently refer it to a genus, and should currently remain as Teleosauroidea indeterminate.

In addition, Fara et al. (2002) briefly described a fragmentary portion of premaxilla, KE-222-1, from the Techout Formation (Bathonian) and attributed it to *Steneosaurus* sp. The associated tooth is described as gracile, yet conical. However, the specimen figures are too dark to confidently identify KE-222-1 as either *Yvridiosuchus* or *Deslongchampsina*. Therefore, we attribute KE-222-1 to Teleosauroidea indeterminate.

1.4 Morphotypes within the Bathonian of the UK

We have established, primarily based on tooth and cranial morphology, that there were two distinct morphotypes present during the Bathonian of England, both preserved in Great Oolite Group: a durophagous/macrophagous morphotype (*Yvridiosuchus boutilieri*) and an intermediate mesorostrine form (*Deslongchampsina larteti*) that falls between piscivorous and macrophagous morphologies (e.g. Foffa et al., 2018a). However, there is also the presence of a third morphotype within the Great Oolite Group, *Steneosaurus megistorhynchus* (OUMNH J.1414; Fig. 12A). A longirostrine lower jaw, with two erupting

teeth, represents this taxon. *Steneosaurus megistorhynchus* (OUMNH J.1414) differs from *D. larteti* (OUMNH J.29851) and *Y. boutilieri* (OUMNH J.29850) in the following:

1. The overall construction of OUMNH J.1414 is much more slender and gracile compared to *Y. boutilier*i (OUMNH J.29850), as well as *D. larteti* (OUMNH J.29851);
2. In OUMNH J.1414, the teeth are pointed, small, slender, and mediolaterally compressed. In *Y. boutilieri* (OUMNH J.29850), the teeth are conical, blunt and anastomosed, and in *D. larteti* (OUMNH J.29851), they are robust and are not mediolaterally compressed;
3. In OUMNH J.1414, the carinae on the teeth are small and faint, whereas in *Y. boutilieri* (OUMNH J.29850), the carinae are pronounced and noticeable;
4. The anterior reception pits of the mandible are small and nearly unnoticeable in OUMNH J.1414, whereas in *Y. boutilieri* (OUMNH J.29850) the reception pits are deep and extensive throughout the mandible; and
5. The angular is gently dorsoposteriorly curved in OUMNH J.1414, as opposed to *Y. boutilieri* (OUMNH J.29850) in which the angular is sharply dorsoposteriorly curved.

Overall, *S. megistorhynchus* is more similar in form to *S. leedsi* (e.g. NHMUK PV R 3320, NHMUK PV R 3806) than *D. larteti* (OUMNH J.29851) or *Y. boutilieri* (OUMNH J.29850); due to its slender build and teeth, *S. megistorhynchus* (OUMNH J.1414) might possibly have been a piscivore and/or teuthophage. In addition, Lydekker (1888) mentions the presence of *Teleosaurus cadomensis* from Fuller's Earth (Bathonian) of Calvados, France (the area where the holotype of *D. larteti* was found). Known from an array of specimens (e.g. NHMUK PV R 119a [Fig. 12B]; NHMUK PV R 880a; NHMUK PV OR 32584;

NHMUK PV OR 32588; NHMUK PV OR 32591), *T. cadomensis* is a longirostrine, heavily armoured, more terrestrial form. In sum, we can now recognize four distinct ecomorphotypes living at the same time in the same geographical area, but occupying different niches.

An interesting observation to note is that while Sub-Boreal teleosauroid ecosystems of England change in diversity through time, the ecological structuring (which has briefly been explored; see Hua, 1997; Hua & Buffetaut, 1997; Foffa et al., 2018a), in particular during the Bathonian-Callovian, remains relatively similar. Prior to the Bathonian, in the Toarcian Whitby Mudstone Formation of England, '*Steneosaurus*' *brevior* represents a mesorostrine generalist, *Steneosaurus bollensis* a longirostrine generalist, and *Steneosaurus gracilirostris* a longirostrine specialist with lateral orbits (likely a piscivore) (Westphal, 1962). In addition, the continental Toarcian deposits of Luxembourg and Germany had a slightly different diversity: a mesorostrine generalist ecomorph ('*Steneosaurus*' *brevior*), a longirostrine generalist ecomorph (*Steneosaurus bollensis*) and a heavily armoured, more terrestrial ecomorph (*Platysuchus multiscrobiculatus*) (Westphal, 1962; Johnson et al., 2018; Sachs et al., in review).

By the Bathonian (Cornbrash Formation), all teleosauroids had dorsal/dorsolaterally oriented orbits, so the niche held by *S. gracilirostris* was apparently lost. However, a new ecomorphotype evolved: a mesorostrine macrophage/durophage (represented by *Yvridiosuchus boutilieri*). In the Bathonian, the heavily armoured, more terrestrial longirostrine ecomorphotype was filled by *Teleosaurus cadomensis*, *Deslongchampsina larteti* filled the role of mesorostrine generalist, and *Steneosaurus megistorhynchus* replaced *S. bollensis* as the longirostrine generalist. In the mid-Callovian (Oxford Clay Formation), *Y. boutilieri* gave way to *Lemmysuchus obtusidens* as the mesorostrine macrophage/durophage form; *Steneosaurus edwardsi* replaced *D. larteti* as the mesorostrine generalist (and is

currently the most commonly known teleosauroid from the Oxford Clay); *Steneosaurus leedsi* represented the longirostrine generalist ecomorph; and *Mycterosuchus nasutus* filled the more terrestrial, longirostrine role. In the Late Jurassic, during the Kimmeridgian-Tithonian, macrophagous/durophagous ecomorphs were the most dominant form of teleosauroids, with *Machimosaurus mosae*, *Machimosaurus hugii* and *Machimosaurus buffetauti* occupying these roles, and the rarer, mesorostrine generalist form was represented by *Steneosaurus bouchardi* Sauvage, 1872. Interestingly, there was also a shift to more pelagic forms, which included taxa such as *Aeolodon priscus*, *Bathysuchus megarhinus* (Foffa et al., in press) and *Steneosaurus jugleri* Meyer, 1845. In addition, the heavily armoured, more terrestrial and longirostrine generalist ectomorphs vanished.

The Bathonian-aged *Yvridiosuchus boutilieri* also represents the current oldest known member of Machimosaurini from England, and the current oldest substantial machimosaurin material from anywhere in the world. This shows that, while rare, machimosaurins were already an important component of Bathonian ecosystems and had already evolved key characteristic machimosaurin features earlier than originally thought (i.e. blunt anastomosing teeth, parallelogram-shaped supratemporal fenestrae, deep reception pits).

Conclusions

While '*Steneosaurus*' *larteti* and '*Steneosaurus*' *boutilieri* are both morphologically and historically important teleosauroid taxa, little work has been done on them since the mid-20th century. Here we re-describe one complete specimen of '*S.*' *larteti*, OUMNH J.29851, consisting of a nearly complete skull, and use it to establish a new genus, *Deslongchampsina*.

We then re-describe four specimens of '*S.*' *boutilieri* (the designated neotype consisting of a partial skull; one complete skull and nearly complete mandible; one nearly complete skull; and one partial mandible) and designate a new genus, *Yvridiosuchus*. *Yvridiosuchus* and *Deslongchampsina* represent two distinct Bathonian morphotypes (along with *Steneosaurus megistorhynchus* as a third morphotype) in the Cornbrash Formation of England, which are joined by a fourth coeval morphotype from Fuller's Earth of France (*Teleosaurus cadomensis*): *Yvridiosuchus* was a mesorostrine macrophagous form, *S. megistorhynchus* a longirostrine generalist/piscivorous form, *Deslongchampsina* an intermediate, mesorostrine generalist form and *Teleosaurus* a more terrestrial longirostrine ecomorphotype. In addition, many of the defining characteristics of Machimosaurini had already evolved by the Bathonian, suggesting that the transition from a generalist diet to more macrophagous/durophagous one began prior to the Bathonian. This is supported by the broad distribution of machimosaurins in the Bathonian, known from the Sub-Boreal seaways north of the Tethys (England and France) and southern shore of the Tethys/Proto-Atlantic (Morocco). The poor fossil record of teleosauroids in the Aalenian and Bajocian hampers our understanding of when this major evolutionary innovation began, and when members of Machimosaurini achieved their circum-Tethys distribution.

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Figures.

Figure 1. Photographs (A, C, E, G, I, K) and line drawings (B, D, F, H, J) of *Deslongchampsia larteti* (Eues-Deslongchamps, 1866) **comb. nov**., OUMNH J.29851, neotype. Skull in dorsal (A-B), palatal (C-D), left (E-F) and right (G-H) lateral, and occipital (I-J) views. Tooth of left P3 in right anterolabial (K) view. Darker shading represents matrix. Note the large antorbital fenestrae. Refer to the main text for the abbreviations list. Scale bars: 5 cm (A, C, E, G, I) and 3 cm (K).

Figure 2. Photographs of Machimosaurini indeterminate, (A) OUMNH J.1406 and (B) OUMNH J.1417. Refer to the main text for the abbreviations list. Scale bars: 5 cm.

Figure 3. Photograph (A, C) and line drawing (B, D) of *Yvridiosuchus boutilieri* (Eudes-Deslongchamps, 1868) **comb. nov**., OUMNH J.1401, neotype. Skull in dorsal (A-B), palatal (C-D), and right (E-F) and left (G-H) lateral views. Lighter shading indicates plaster, and darker shading represents matrix. Refer to the main text for the abbreviations list. Scale bars: 5 cm.

Figure 4. Photographs (A, C, E, G, I, K, L) and line drawings (B, D, F, H, J) of *Yvridiosuchus boutilieri* (Eudes-Deslongchamps, 1868) **comb. nov**., OUMNH J.29850, referred specimen. Skull in dorsal (A-B), palatal (C-D) left (E-F) and right (G-H) lateral, and occipital (I-J) views. Left retroarticular process (K) in left lateral view, and maxillary tooth (L) in labial view. Note the anastomosing pattern at the apex of the tooth (L). Refer to the main text for the abbreviations list. Scale bar: 5 cm (A-K) and 1 cm (L).

Figure 5. Photographs (A, C, E, G) and line drawings (B, D, F, H) of *Yvridiosuchus boutilieri* (Eudes-Deslongchamps, 1868) **comb. nov**., OUMNH J.1403 (A-F) and OUMNH J.1404 (G-H), referred specimens. Skull in dorsal (A-B), palatal (C-D) and occipital (E-F) views, and

partial mandible (G-H) in dorsal view. Darker shading represents matrix. Refer to the main text for the abbreviations list. Scale bars: 5 cm.

Figure 6. Results of the phylogenetic analysis, focusing on the positioning of *Yvridiosuchus boutilieri* and *Deslongchampsina larteti*. (A) Simplified strict consensus trees of the 201 most parsimonious trees; (B) simplified majority rules trees, and (C) simplified strict consensus tree with implied weighting (k = 12) of the 201 most parsimonious trees of Teleosauroidea within Crocodylomorpha.

Figure 7. Comparative plate of the neurovascular foramina of the premaxilla and anterior maxilla in: (A) *Steneosaurus heberti* (MNHN.F 1890-13); (B) *Deslongchampsina larteti* (OUMNH J.29851); (C) '*Steneosaurus*' *brevior* (NHMUK PV OR 14781); (D) *Yvridiosuchus boutilieri* (OUMNH J.29850); and (E) *Lemmysuchus obtusidens* (LPP.M.21). All specimens in left lateral view. Scale bars: 1 cm.

Figure 8. Comparative plate of the tooth morphology in: (A) *Deslongchampsina larteti* (OUMNH J.29851); (B) *Steneosaurus heberti* (MNHN.F 1890-13); (C) *Steneosaurus edwardsi* (PETMG R178); (D) *Yvridiosuchus boutilieri* (OUMNH J.29850); (E) *Lemmysuchus obtusidens* (NHMUK PV R 3168); and (F) *Machimosaurus buffetauti* (SMNS 91415). Scale bars: 1 cm.

Figure 9. Comparative plate of the anterior rostrum of (A) *Deslongchampsina larteti* (OUMNH J.29851); (B) *Steneosaurus leedsi* (NHMUK PV R 3806); (C) *Yvridiosuchus boutilieri* (OUMNH J.1401); (D) the Chinese teleosauroid previously referred to as *Peipehsuchus* (IVPP V 10098); (E) *Steneosaurus heberti* (MNHN.F 1890-13); and (F) *Lemmysuchus obtusidens* (LPP.M.21). Note the lack of constriction in *D. larteti*. Scale bars: 3 cm.

Figure 10. Comparative plate of the presence of absence of antorbital fenestrae in: (A) *Steneosaurus gracilirostris* (NHMUK PV OR 14792); (B) *Deslongchampsina larteti* (OUMNH J.29851); (C) *Yvridiosuchus boutilieri* (OUMNH J.1401); (D) *Steneosaurus heberti* (MNHN.F 1890-13); and (E) *Lemmysuchus obtusidens* (PETMG R39). Note that *S. heberti* and *L. obtusidens* lack antorbital fenestrae, and that the fenestra is small in *Y. boutilieri*. Scale bars: 4 cm.

Figure 11. Comparative plate of (A) *Steneosaurus stephani* (NHMUK PV OR 49126); (B) *Yvridiosuchus boutilieri* (OUMNH J.1401); and (C) *Deslongchampsina larteti* (OUMNH J.12951). Scale bars: 4 cm.

Figure 12. Photographs of (A) *Steneosaurus megistorhynchus* (Eudes-Deslongchamps, 1866), OUMNH J.1414 and (B) *Teleosaurus cadomensis* (Lamouroux, 1820), NHMUK PV R 119a. Refer to the main text for the abbreviations list. Scale bars: 5 cm.